

PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

161st Session (1948-49)

Vol. 161

Part 1

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PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

Session 1948-49

Vol. 161

Part 1

PROCEEDINGS OF THE GENERAL MEETING ON 14 October 1948

Prof. G. R. DE BEER, F.R.S., President,
in the Chair.

The Proceedings of the Anniversary Meeting held on Monday, 24 May 1948, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Mr. A. H. G. Alston, Dr. R. E. G. Armattoe, Mr. J. M. Black, Miss W. M. A. Brooke, Mr. I. H. Burkill, Prof. G. R. de Beer, Mr. J. R. Dibb, Dr. O. R. Gurney, Dr. Helga S. Hacker, Mr. James Hornell, Mr. D. J. MacDonald, Mr. S. A. Manning, the late Miss F. H. B. Marsh, Dr. Cecil Miles, Mr. A. A. Pearson, Mr. C. T. Prime, Dr. T. A. Sprague, Mr. W. G. Templeman, Dr. C. G. G. J. van Steenis, Mr. B. Verdcourt, Dr. J. C. Willis, the Bedfordshire Natural History Society, the British Council, the Royal College of Surgeons of England, the National Central Library and the National Museum of Wales, Cardiff.

The following Fellows signed the Obligation in the Roll and Charter Book, and were Admitted Fellows:—Dr. Roger Bevan, Dr. Madhab Chandra Das, Mr. Alan Fisk, Professor Kenneth James Franklin, Mr. Arthur George Lee Hellyer, Mr. John Withers Lester, Mr. James Wilmot Ogden Platt, Miss Ellen Mary Stephenson and Mr. George Stanley Woodcock.

The President reported the deaths of Miss Florence Hannah Bacon Marsh, Dr. Leonard Richmond Wheeler, Mr. William Bathgate Cranfield, Fellows; and Mr. Alfred Santer Kennard, Associate.

The following communication was read and discussed:—

Dr. JOSEPH PEARSON, F.L.S. The Marsupial Placenta. (Discussed by Prof. J. P. Hill, Prof. C. J. van der Horst, Prof. E. C. Amoroso, Dr. S. M. Manton, Dr. Edward Hindle and the President; Dr. Pearson replied.) [An extended abstract is printed below.]

PLACENTATION OF THE MARSUPIALIA

By Dr. JOSEPH PEARSON.

The surface of the blastocyst consists of four areas, each of which may contribute to placentation. These are, in order of their appearance and in the correct sequence of their increasing efficiency:

Chorion, formed of trophoblast and somatic mesoderm. (Chorionic placenta—non-vascular.)

Bilaminar omphalopleure, formed by the apposition of trophoblast and yolk-sac endoderm. (Bilaminar vitelline placenta—non-vascular.)

Vascular omphalopleure, formed by the growth of somatic and splanchnic mesoderm between the trophoblast and yolk-sac endoderm. (Chorio-vitelline placenta—vascular.)

Allantochoion, usually formed by the apposition of the chorion and the allantoic endoderm with its enveloping layer of splanchnic mesoderm. (Chorio-allantoic placenta—vascular.)

It should be observed that the trophoblast, with its phagocytic, histiotrophic and haemotrophic properties is a fundamental component of all four, and that the splanchnic mesoderm, which is the seat of the foetal blood system, is a necessary part of both vascular types of placenta.

It is likely that these several types may operate in regular sequence in the same animal with a time overlap of two contiguous types in the sequence. This is probably true of all viviparous mammals.

In the Metatheria (Marsupials) the yolk-sac is the dominant organ of placenta, and even in the Eutheria ('placental' mammals) the yolk-sac is in most instances large and important until the allantois is fully formed.

In the Marsupials the placenta is variable and may be grouped as follows, though it should be noted that this grouping has no relation to phylogenetic affinities.

(1) Yolk-sac large throughout foetal life. Bilaminar vitelline and chorio-vitelline placenta.

Allantois small and does not reach the chorion. (Didelphidae, Potoroidae, Macropodidae, Phalangeridae.)

(2) Yolk-sac and yolk-sac placenta as in No. (1).

Allantois small, reaches the chorion and then recedes from it. (*Dasyurus*.)

(3) Yolk-sac and yolk-sac placenta as in Nos. (1) and (2).

Allantois small, reaches the chorion and remains attached to it throughout foetal life. (*Phascogalea*, *Vombatus*.)

(4) Yolk-sac large and persistent throughout foetal life. Yolk-sac placenta in early stages.

Allantois small, reaches the chorion and forms a chorio-allantoic placenta. (Peramelidae.)

The unusual and variable condition of Marsupial placenta is considered by most embryologists to indicate that the dominance of the yolk-sac and the minor part played by the allantois is a secondary condition and that the recent Marsupials show varying degrees of retrogression from an earlier condition in which the allantois became fully placental.

Hubrecht and Flynn drew attention to the similarity between the placenta of *Perameles* and that of the dog. Hence Hubrecht considered that the Marsupials were descended from Eutherian stock while Flynn postulated an ancestral form common to both Metatheria and Eutheria in which the allantoic placenta possessed a phagocytic trophoblast. Hill, on the other hand, considers that the common ancestors of the Metatheria and Eutheria had a simple epitheliochorial placenta with a non-phagocytic trophoblast and that this placenta was shared equally by the yolk-sac and allantois; and that the placenta of *Perameles* is unlike anything found elsewhere in the Mammalia and is probably a convergent structure.

In view of these conflicting opinions, there appear to be good reasons for re-examining the whole question of Marsupial placenta.

If we may regard the Monotreme condition as being comparable to a stage in the evolution of Mammalian viviparity in which the egg was fast losing its food-yolk (and not, as Hubrecht claimed, as a secondary reversion from viviparity to oviparity), then it would appear that the predominant cause of Mammalian viviparity was the inadequacy of the food-yolk supply. (By contrast many reptiles, though still in possession of an abundant supply of food-yolk, have become viviparous for climatic reasons.) In the Monotremes

the chorion probably acts as an agent for the absorption and transmission of solid and liquid food materials to the developing embryo during its passage down the oviduct. The yolk-sac and allantois both function as in oviparous Amniotes.

If the food-yolk supply were reduced still further, the inefficient chorionic 'placenta' would then be supplemented by the bilaminar omphalopleure, and the allantois, still in contact with the chorion, would continue to act as a respiratory organ. With a further reduction in the food-yolk supply, the yolk-sac would increase in size so as to provide a larger absorptive surface. In the course of these changes, the vascular omphalopleure would gradually assume important nutritional and respiratory functions. The abnormal growth of the yolk-sac would tend to prevent the more tardily developed allantois from reaching the chorion, and the function of respiration would then be taken over by the vascular omphalopleure. Thus a condition would be reached similar to that found in most recent Marsupials in which the allantois lies in the splanchnocoele some distance from the chorion. Hubrecht regarded this as the 'retreat' of a fully placental allantois from the chorion, but in the view now presented it is suggested that it is merely the non-placental, respiratory allantois of the oviparous Amniotes which, under conditions brought about by the change to viviparity, has been prevented by the abnormal growth of the yolk-sac from reaching the chorion.

It does not necessarily follow that the evolution of the Eutherian placenta passed through a stage in which the yolk-sac dominated foetal life as it does in recent Marsupials. But we cannot ignore the fact that in most recent Eutherians, which have a highly organized and efficient allantoic placenta, there is a stage in early foetal life during which the yolk-sac is large and has placental functions. The possibility of a dominant yolk-sac placental phase having occurred in the earlier stages of Mammalian viviparity cannot, therefore, be ignored.

It is doubtful whether the reptilian type of placentation can throw much light upon the Marsupial problem. In the viviparous reptiles the yolk-sac is almost entirely concerned with its primitive function as a food reservoir and the yolk-sac decreases in size as the food is absorbed. The allantois, therefore, reaches the chorion without hindrance and, in those cases in which the food-yolk supply is inadequate, assumes full placental functions. The circumstances are vastly different in the Mammalia where, so far as can be said, true viviparity resulted from an inadequate supply of food-yolk. It may even be the case that viviparity may have arisen independently on more than one occasion within the Mammalia and that the Marsupial type may have no close relationship with that of the Eutheria, though this is doubtful. The variable types of placentation found in the Marsupialia are not based upon phylogenetic relationships, e.g. the primitive *Didelphis* and the highly specialized rat-kangaroos have the same placental condition.

To sum up :

(1) The absence of allantoic placentation in most Marsupials is unlikely to be the result of a secondary abbreviation of foetal life, but may simply be due to the fact that viviparity in this group has not passed beyond an early stage.

(2) It is improbable that a group of Mammals, once having acquired an efficient allantoic placentation would revert to the inadequate placentation provided by the yolk-sac.

(3) The rather complex placenta of *Perameles* may be nothing more than another Marsupial instance of convergence.

Discussion,—

The allantoic Placenta of *Perameles*.

(Plate 1.)

Professor J. P. HILL, in demonstrating a series of lantern slides illustrating the development and structure of the allantoic placenta of *Perameles*, pointed

out that this placenta is unique amongst Mammalian placentas, in that its basis arises by the fusion of two epithelial layers, respectively foetal and maternal, to form a single conjoint layer, actually a syncytium, which remains preserved up to the time of the birth of the young one. The maternal constituent of the placenta is furnished by the uterine epithelium and the underlying capillaries. The epithelium by the fusion of its constituent cells, early becomes transformed into a relatively thick syncytial layer, produced below into a series of close-set lobules, in which the epithelial nuclei come to lie in nests and between which maternal capillaries penetrate upwards to form eventually a fine capillary plexus just below its surface. This layer we shall speak of as the maternal syncytium. The foetal constituent of the allantoic placenta is provided by the trophoblastic ectoderm or trophoblast of the allanto-chorion (i.e., the discoidal area of the chorionic membrane with which the allantois carrying the allantoic vessels of the embryo fuses) and by the allantoic capillaries formed by the latter vessels, which directly overlie the trophoblast.

In the earliest stage of placental formation available for study (*P. nasuta*, with embryos of G.L. 5.7 and 6.8 mm.), the trophoblast of the allanto-chorionic area (Plate 1, fig. 1, *c.tr.*) is seen to be markedly thickened and to have become more or less closely approximated to the surface of the already well developed maternal syncytial layer (*m.syn.*). From its deep surface, next the latter, dark staining single cells and small multinucleate syncytial masses are in process of becoming detached. These are endowed with invasive properties and when they come into contact with the surface of the maternal syncytium, they actively penetrate into it and fuse with it. Their cytoplasm becomes incorporated in that of the latter, whilst their nuclei migrate downwards and eventually come to lie in the nests of maternal epithelial nuclei occupying the lobules (fig. 1, *m.n.*), where they are readily distinguishable from the maternal by their more deeply staining character and later on, by their larger size. This stage accordingly, marks the commencing formation of the conjoint syncytial layer of the placenta but as yet only a small number of trophoblastic nuclei have penetrated into the maternal nuclear nests (fig. 1, *tr.n.*).

The above mentioned invasive trophoblastic elements collectively may be regarded as the equivalent of the syncytio-trophoblast of Eutherian Mammals, whilst the parent layer corresponds to the cyto-trophoblast of these. Flynn (1923) was the first to recognize that the allanto-chorionic trophoblast in *Perameles* becomes distinguishable into syncytial and cellular portions which he designated plasmodiblast or plasmoditrophoblast and cytoblast or cytotrophoblast respectively.

In the next stage demonstrated (*P. nasuta*, with embryo G.L. 7 mm.) very substantial progress in placental development has taken place. In the interval, the trophoblast has become intimately fused with the conjoint syncytium (now established as such) as the result of the active production by the parent layer or cyto-trophoblast of invasive syncytio-trophoblastic elements. Fig. 2 is taken from the peripheral region of the placenta and shows an area where the parent cyto-trophoblast (*c.tr.*) is still present as a light staining layer of high columnar cells with large chromatin-rich nuclei. It rests on, and in places is continuous with a darkly stained, rather ill-defined zone of cytoplasm, of very irregular thickness, in which are situated numerous darkly stained nuclei (*s.tr.*). This zone is formed of syncytio-trophoblast which has fused with the superficial portion of the original maternal syncytium. Its cytoplasm merges without limit into the rather lighter staining cytoplasm of the deep lobular zone of the conjoint syncytium, and whilst many of its nuclei still lie superficially close below the cyto-trophoblast, others are in process of migrating down to enter the nuclear nests of the lobular zone. These nests are very variable in their constitution. In many of them the light staining maternal nuclei (fig. 2, *m.n.*) predominate, with only a relatively small admixture of trophoblastic nuclei (*tr.n.*), but in others the latter are the more numerous.

In the more central portions of the placental area, the stages leading to the all but complete incorporation of the cyto-trophoblast layer itself in the conjoint syncytium can be followed. It loses its high columnar character and becomes reduced to a discontinuous layer of plump, irregularly cuboidal cells possessing one, two or more nuclei. With or without previous fusion with each other, they become continuous below with the cytoplasm of the conjoint syncytium and finally, becoming deeply staining, they lose their identity and become incorporated in the latter, though forming for a time a deeply staining nucleated zone at its surface.

Later stages show, however, that quite a considerable number of cyto-trophoblast cells fail to fuse with the conjoint syncytium and persist on its surface as isolated deeply staining cells.

The succeeding stage (*P. obesula*, with embryo G.L. 8.75 mm. illustrated in fig. 3, is of particular importance since the allantoic placenta is now fully constituted and capable of carrying out its primary function of subserving the greatly increased respiratory needs of the rapidly growing embryo during the remainder of the gestation period.

Prior to this stage, the nutritional and respiratory requirements of the growing embryo have been met and indeed continue to be met in considerable measure, by the relatively simple yolk-sac or omphalopleural placenta, constituted by the close apposition of the vascular and bilaminar portions of the omphalopleure or yolk-sac wall with the purely maternal syncytial layer which lines the rest of the uterus outside the allantoic placental area.

The attainment of functional activity by the allantoic placenta in this stage is the outcome of the all but complete fusion of the allanto-chorionic trophoblast with the maternal syncytium to form the conjoint syncytium and its consequent disappearance as a continuous layer. As the result, the allantoic capillaries (fig. 3, *all.c.*) now much more richly developed than in the preceding stage, are enabled to come into direct and intimate contact with the furrowed surface of the syncytium immediately below which the maternal capillaries (fig. 3, *m.c.*) have now formed a rich capillary plexus. In this way, the two blood streams, foetal and maternal, become closely approximated and respiratory exchanges between the two can readily be effected.

The conjoint syncytium, somewhat thicker on the average than that of the preceding stage, differs from it in three respects; its cytoplasmic basis stains fairly uniformly throughout, its nuclei are largely concentrated in the nuclear nests and it is more richly vascularised. In the nests, the large, deeply staining trophoblastic nuclei (fig. 3, *tr.n.*) are readily distinguishable from the small, clear, inactive-looking maternal nuclei (*m.n.*) which tend to be aggregated in the deeper portions of the nests.

In the later stage (*P. obesula*, embryo G.L. 10 mm.), illustrated in fig. 4, apart from an increase in its vascularity, the most striking feature in the placenta is the general increase in the size and staining capacity of the trophoblastic nuclei (fig. 4, *tr.n.*) in the nests, many of them being quite large and markedly hypertrophied. They lie closely-packed together and in the larger nests especially, are still accompanied by numbers of small, clear maternal nuclei (fig. 4, *m.n.*) which appear quite well preserved.

In the still later stage (*P. obesula*, embryo G.L. 12.5 mm.) the nests present a strikingly different appearance to those just described. Here, as the result of the amitotic division and fragmentation of the hypertrophied trophoblastic nuclei, many of the nests have come to be composed of a few large nuclei, together with numerous smaller nuclei which vary greatly in size and in staining capacity, many of them, indeed, staining so intensely that they might be described as pycnotic. Moreover, the nuclei, instead of forming compact nests, tend to be arranged in loose, open groups and to spread out irregularly into the surrounding cytoplasm. Evidently we have here to do with the onset of degeneration in the trophoblastic nuclei, and in this connection it is interesting

to find that already the maternal nuclei have more or less completely disappeared.

The allantoic placenta, it may be noted, is in functional activity along with the omphalopleural placenta, from the stage of the embryo just over 8 mm. in length to that of the full-term foetus which is born when it has attained a length of about 14 mm.

Finally Professor Hill recalled that in his original account of the *Perameles* placenta in 1897, he concluded that the allanto-chorionic trophoblast simply degenerated and disappeared. This conclusion was contested by Hubrecht in 1908 and by Flynn in 1923 and he himself in 1929, as the outcome of a study of new material and a re-examination of the old, acknowledged his previous error and confirmed the conclusion of the just mentioned investigators that fusion of the allanto-chorionic trophoblast with the maternal syncytial layer does actually occur in the way described. Because of the unique condition thus arising, and for other reasons, he had come to the conclusion that the allantoic placenta of *Perameles* had been evolved quite independently, within the limits of the order Marsupialia, if not indeed, of the family Peramelidae, and that consequently it did not possess the primitive significance he originally ascribed to it. He now regarded the simple apposed chorio-allantoic-omphalo pleural placenta as seen in *Phascolarctos* and *Phascolomys* as the most primitive type amongst the Marsupialia and he suggested that from such a type, the more advanced placentation of *Perameles* might well have been evolved, whilst from it also, the exclusively omphalopleural or yolk-sac placenta, characteristic of the Didelphids, Dasyurids and Macropods might have arisen as secondary, divergent variations, the result of the loss by the allantois of its primary respiratory function. He was unable to accept Dr. Pearson's suggestion as to the cause of that loss or to agree with his belief that the placentation of the 'prototypal' Marsupial was effected solely by means of the yolk-sac. Nor could he agree with his thesis that placentation is not a safe guide to phylogeny. In his opinion, the facts yielded by comparative placental studies, properly used, furnished most valuable guidance in the tracing of Mammalian inter-relationships.

EXPLANATION OF PLATE 1.

List of reference letters.

all.c., allantoic capillary. *all.end.*, allantoic endoderm. *all.v.*, allantoic vessel. *c.syn.*, conjoint syncytium. *c.tr.*, cyto-trophoblast. *m.c.*, maternal capillary. *m.n.*, maternal syncytial nucleus. *m.syn.*, maternal syncytium. *s.tr.*, syncytio-trophoblast. *syn.l.*, lobule of maternal syncytium. *tr.n.*, trophoblastic nucleus.

Photomicrographs by Mr. F. J. Pittock, F.R.P.S., A.L.S.

FIG. 1.—*P. nasuta*, embryos G.L. 5.7 and 6.8 mm. Section showing the commencing attachment of the trophoblast (*c.tr.*) of the allanto-chorion to the maternal syncytium (*m.syn.*). The trophoblast (cyto-trophoblast) (*c.tr.*) is formed by a layer of narrow columnar cells with mostly large oval nuclei. Projecting from its deep surface on the left are four prospective syncytio-trophoblastic cells with deeply staining cytoplasm and nuclei, to the right of these is a small multinucleate syncytial mass (*s.tr.*) which is attached to, and has already begun to penetrate into the maternal syncytium (*m.syn.*). Note below it and probably derived from it, two deeply stained trophoblastic nuclei which have migrated down into the maternal syncytium, the deeper of the two (*tr.n.*) lying in a nest of maternal syncytial nuclei (*m.n.*). To the right of the syncytial mass (*s.tr.*) is a much smaller mass, with three or four nuclei, also beginning to penetrate and still more to the right, a small and a larger cell are present, the latter in contact with the maternal syncytium. The lobules (*syn.l.*) of the maternal syncytium with their nests of light staining nuclei (*m.n.*) are clearly seen, as also are the maternal capillaries (*m.c.*) which have penetrated into the syncytium. $\times$ about 275.

* In both these genera, the allantois is well-developed and fuses with the chorion to form a richly vascularised discoidal area of allanto-chorion.

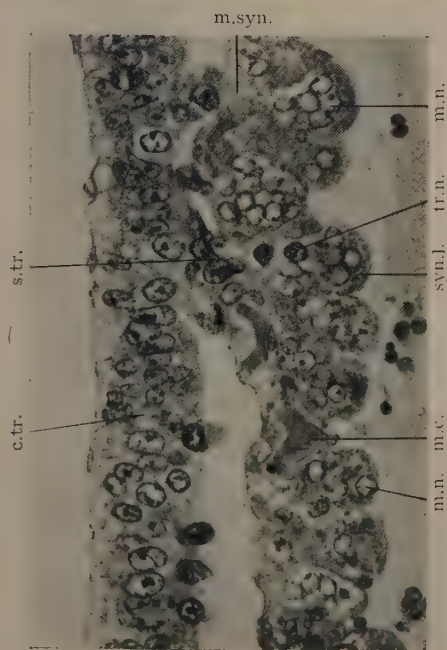


FIG. 1.

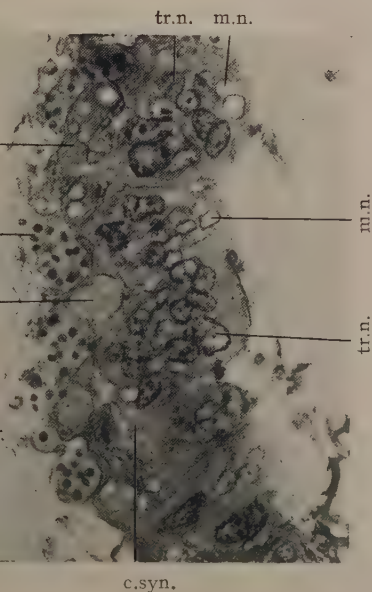
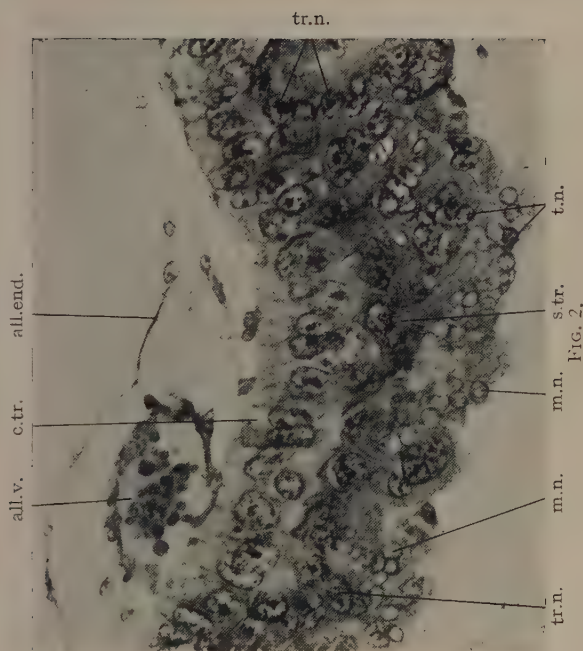


FIG. 3.

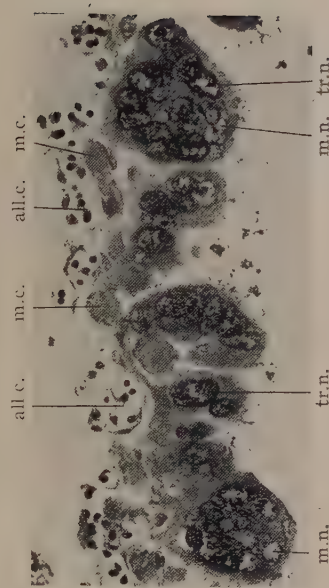


FIG. 4.

The allantoic placenta of *Perameles*.

FIG. 2.—*P. nasuta*, embryo G.L. 7 mm. Section through the peripheral region of the allantoic placenta showing the cyto-trophoblast (*c.tr.*) as a continuous thick layer of columnar cells, resting on, and in places continuous with an underlying very irregular zone of darkly stained cytoplasm (*s.tr.*) containing numerous deeply staining nuclei (*tr.n.*), and representing the syncytio-trophoblast fused with the conjoint syncytium, now well established. Many of the syncytio-trophoblastic nuclei (*tr.n.*) still lie in the superficial portion of the zone, close below the cyto-trophoblast, others are migrating down to enter the nuclear nests in the deep lobular zone of the syncytium. These nests vary in their nuclear constitution, in many, the light staining maternal nuclei (*m.n.*) are more numerous than the much more deeply staining trophoblastic (*tr.n.*) but in others, the reverse is the case. $\times$ about 250.

FIG. 3. *P. obesula*, embryo G.L. 8.75 mm. Section through the allantoic placenta, showing its structural appearance when it is established and in functional activity. Owing to the incorporation of the trophoblast in the conjoint syncytium, the allantoic capillaries (*all.c.*) now much more richly developed than in the preceding stage, have been enabled to come into direct and intimate contact with the irregularly furrowed surface of the conjoint syncytium, immediately below which the maternal capillaries (*m.c.*) have now formed a fine capillary plexus. The cytoplasmic matrix of the conjoint syncytium (*c.syn.*) now stains fairly uniformly throughout and the great majority of the trophoblastic nuclei have become concentrated in the nuclear nests. These nuclei (*tr.n.*) are readily distinguishable by their large size and deeply staining character, from the small clear, inactive-looking maternal nuclei (*m.n.*) which are still numerous in many of the nests. $\times$ about 300.

FIG. 4. *P. obesula*, embryo G.L. 10 mm. Section of the allantoic placenta, at a later stage than that of fig. 3, showing its general structure and in particular the increase which has taken place in the size and staining capacity of the trophoblastic nuclei (*tr.n.*) in the nuclear nests, many of them being large and distinctly hypertrophied. Maternal nuclei (*m.n.*) are still present in varying numbers in many of the nests, and appear quite well preserved. $\times$ about 250.

Professor E. C. AMOROSO after expressing his appreciation of Dr. Pearson's communication, said he could not agree that placentation was not a safe guide to phylogeny. Evolution of the foetal membranes was a fact and if, as Professor Hill had pointed out, one could evaluate their characters properly, they might be used to throw light on the phylogenetic relationships of the various groups. It was clear that there were still major gaps in our knowledge of the structure, physiology and mode of development of the placenta of most marsupials, particularly in such primitive genera as *Thylacinus* and *Sarcophilus*. Consequently, the validity of Dr. Pearson's viewpoint—the occurrence of an exclusively omphalopleural phase in the earlier stages of Mammalian viviparity—could not be regarded for the present as being conclusively demonstrated.

One aspect of the subject of placentation which might be expected to yield information regarding the evolution of viviparity is the study of placental hormones. A wealth of experimental evidence has been accumulated in support of the view that the placenta has become specialized as an endocrine organ during the evolution of viviparity in mammals. One of the problems that confronted mammals in the evolution of viviparity was that of retaining embryos in the uterus for a time beyond the limits of the normal oestrous cycle. In both Monotremata and Marsupialia the situation seems to be one in which the length of gestation is comparable to that of a pseudopregnant period or normal luteal phase and there is some evidence that expulsion of the eggs and young is correlated with involution of the corpora lutea. Under such a situation it seems unnecessary to postulate that hormones other than those regulating the oestrous cycle take part. In the Eutheria, however, it appears that the placenta gradually assumes certain pituitary and ovarian functions and thus enables the period of gestation to extend beyond the limits of a normal oestrous cycle. The secretion of gonadotropins, oestrogens, and progesterone by the placenta has been described for several species: monkey, human being, mare and rat. When the adoption of pituitary and gonadal functions by the placenta

is considered from an evolutionary standpoint it seems reasonable to suppose that the process might have followed somewhat divergent paths in different mammalian groups. The stimulation of luteal secretion is the only effect known to be produced by the gonadotropin of the rat placenta. That gestation in the rat cannot continue in the absence of the ovaries seems to imply that the placenta does not play an important rôle in the secretion of oestrogen and progesterone. The situation in the mare and in primates differs from that described for the rat in that the placenta secretes oestrogens and progesterone in addition to gonadotropin, and has assumed endocrine control of gestation so completely that during the second half of pregnancy ovariectomy neither interrupts pregnancy nor decreases the amount of oestrogen excreted in the urine.

The importance of these observations as contributions to our knowledge of the evolution of viviparity must remain an open question until such studies have been extended to other mammalian groups. However, the available facts seem to imply that the elaboration of a gonadotropin by the placenta was the initial adaptation which made it possible to extend the period of gestation beyond the limits of the oestrous cycle, while secretion of oestrogen and progesterone represents a further placental specialization allowing a still longer gestation period.

Dr. S. M. MANTON expressed her appreciation of Dr. Pearson's lecture, and raised three points concerning comparisons with Invertebrates. (1) The species of *Peripatus* show a series of conditions which parallel in a remarkable way the vertebrates which Dr. Pearson has considered. An oviparous yolky-egged habit is now largely replaced by a viviparous one in many parts of the world. Some viviparous forms show a yolk-sac filled with yolk, while in others a very large empty yolk-sac is closely applied to oviduct walls, and in some cases a structure superficially resembling a placenta is formed. (2) Has the viviparous habit in these Onychophora been initiated in association with cold or altitude, as Dr. Pearson suggests may have been the case in reptiles and mammal-like reptiles? It would be of interest to investigate the invertebrata further in this connection. (3) A large yolk-sac devoid of yolk in a viviparous embryo has been assumed to be a nutritive organ in both *Peripatus* and Marsupials. This assumption is open to question in the Onychophora; several species show a variety of devices resulting in the early reduction or obliteration of the yolk-sac, so that their embryos develop for many months with no special nutritive organ at all. This being so, the presence of a huge empty yolk-sac in related species can hardly be of great nutritional significance.

THE PRESIDENT expressed his appreciation of the very clear exposition given by Dr. Pearson, which raised two problems of fundamental importance in Zoology. The first was, what was the condition of the allantois in the primitive Marsupials, and the second, can the placenta be used for purposes of taxonomic classification. Professor J. P. Hill and Professor Amoroso had referred to the latter: he (the President) would say a few words about the former, and give briefly the reasons why he was unable to follow Dr. Pearson in his contention that the allantoic contact with the chorion in *Perameles* and in Placental Mammals had been independently evolved. The difficulty was that in the undoubted ancestors of the mammals, the reptiles, the allantois was large and reached the inner surface of the chorion, where, indeed, it performed the all-important function of enabling the respiratory exchanges to take place. The ancestors of the mammals, therefore, already possessed a large allantois, and the same is true of the Monotremata. If this was so, then it would be necessary to assume that the ancestral mammals underwent a reduction of the allantois, followed by its re-enlargement, and this appeared to him to be an extravagant

hypothesis, without sufficient evidence to justify it. Furthermore, there was evidence derived from other organ systems which proved incontrovertibly that the Marsupialia were extremely specialized in their method of reproduction. In the first place, there was the astonishingly immature state of the Marsupial embryo at the time of its birth, which was a specialization associated with the acquisition of the pouch type of milk-feeding. A further consequence of this was the reduction of the milk-dentition in the Marsupials. Here were two features which could only be secondary, and the reduction of the allantois in so many Marsupials could be regarded as a consequence of these features, and could therefore only be regarded as secondary itself. This does not, of course, conflict with the view that the placenta of *Perameles* has been specialized along lines very different from those of Placental Mammals.

PROCEEDINGS OF THE GENERAL MEETING ON 28 October 1948

Professor G. R. DE BEER, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 14 October 1948, having been circulated, were taken as read and confirmed.

The following was thanked for a gift made to the Library since the last Meeting :—Mrs. A. M. Hughes.

The following Fellows signed the Obligation in the Roll and Charter Book and were Admitted Fellows :—Mr. Gerald Anthony Best, Mr. George Soper Cansdale, Dr. John William Jones, Dr. Ivor Isaac, Mr. John William Purseglove and Mr. Donald James Butt White.

The President reported the death of Professor William B. Scott, Fellow of the Society.

The following communication was read and discussed :—

Drs. HELGA S. and H. P. HACKER. Local variation, wandering powers and chances of interbreeding in *Apodemus sylvaticus*, the long-tailed wood mouse. (Discussed by Professor A. C. Hardy, Mr. H. N. Southern, Dr. B. Barnes, Mr. D. H. Chitty, Mr. J. Linn, Professor von Bertalanffy and the President ; Dr. Hacker replied.)

Abstract,—

An interim account was given of records : (a) of the natural travels and homing powers of marked mice caught in 1937 on South Haven Peninsula under a rich variety of local conditions, (b) of marked mouse populations living in a single area in Kent, their differences in size from place to place within the area and from year to year within the period 1937–1943, the growth and survival of individual mice caught at monthly intervals, their longest travels and overlapping ambits, all suggesting absence of closely inbreeding local communities, (c) of the differences in size between populations caught in Kent, Bucks, Dorset, Cornwall and Ireland, the Cornish mice being markedly the largest.

It was shown that winter and summer survival rates are different and that few mice survive from one winter till the next ; that a limit to growth, differing from place to place, is reached in early summer by winter young and in autumn by summer young ; and that the hind feet cease growth early and can therefore

be used as a measure of size. Evidence of local differences in proportions as well as size was not discussed owing to lack of time, but the hope was expressed that the pattern of variation disclosed may throw light on problems of nature and nurture, and may lead to a better understanding of the origin of local races among vertebrates, where the best evidence of evolution comes from fossil skeletons differing in size and shape.

**PROCEEDINGS OF THE GENERAL MEETING ON
25 November 1948**

Professor G. R. DE BEER, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 28 October 1948, having been circulated, were taken as read and confirmed.

The President reported that the Society's congratulations had been conveyed to **Their Majesties The King and Queen** and to **The Princess Elizabeth**, L.G., F.R.S., Hon.Memb.L.S., on the birth of a Prince; and that gracious replies had been received, as follows:—

**To The King's and The Queen's Most
Excellent Majesties.**

MAY IT PLEASE YOUR MAJESTIES,

We, your loyal and dutiful subjects, the President, Council, and Fellows of The Linnean Society of London, beg leave to offer our humble duty and respectful congratulations to Your Majesties on the Birth of a Prince to Her Royal Highness The Princess Elizabeth, and to say how deeply we rejoice that it has pleased Almighty God to bless Your Majesties' House.

Her Royal Highness was graciously pleased to accept Honorary Membership of this Society in May of last year, and thereby conferred on this Society an honour which it holds in highest esteem.

On behalf of The Council and Fellows of
The Linnean Society of London:

L.S.

G. R. DE BEER, *President*,

F. C. STERN, *Treasurer*,

A. TINDELL HOPWOOD, *Secretary*.

15 November 1948.

HOME SECRETARY,
Whitehall,
London, S.W.1.
29th November 1948..

SIR,

I have had the honour to lay before The King the loyal and dutiful Message of the President, Council and Fellows of the Linnean Society of London on the occasion of the birth of a son to Her Royal Highness the Princess Elizabeth, Duchess of Edinburgh and His Royal Highness the Duke of Edinburgh.

I have it in command from The King to convey to you, as President of the Society, the warm thanks of Their Majesties for the kindness and cordiality of these congratulations and good wishes which They were specially pleased to receive on this happy occasion.

I am, Sir,

Your obedient Servant,

[Signed :] J. CHUTER EDE.

The President,
Linnean Society of London.

John Colville, Esq.,
Private Secretary to
Her Royal Highness The Princess Elizabeth, Duchess of
Edinburgh, L.G., F.R.S., Honorary Member of The
Linnean Society of London,
Buckingham Palace,
London, S.W.1.

SIR,

We, the President, Council, and Fellows of The Linnean Society of London, desire to offer to their Honorary Member, Her Royal Highness The Princess Elizabeth, their most respectful congratulations on the Birth of a Prince.

We have the honour to be,

Sir,

Your obedient Servants,

G. R. DE BEER, *President*,

F. C. STERN, *Treasurer*,

A. TINDELL HOPWOOD, *Secretary*.

L.S.

15 November 1948.

BUCKINGHAM PALACE,
16th November 1948.

DEAR SIR,

I am desired by Her Royal Highness The Princess Elizabeth to thank you, the Council, and Fellows of the Linnean Society of London for your very kind congratulations on the Birth of Her Royal Highness' Son.

Yours truly,

[Signed :] A. M. BROWNING,
Comptroller.

The President,
Linnean Society of London,
Burlington House,
Piccadilly, London, W.1.

The following were thanked for gifts made to the Library since the last Meeting :—An anonymous donor, Dr. A. Arber, Mr. G. M. Ash, Rear-Admiral T. P. H. Beamish, C.B., Dr. T. E. T. Bond, Mr. M. Bradshaw Bond, Dr. M. A. Brett, Miss A. McC. Bidder, The Lady Mary Browne, Dr. W. E. Brenchley, O.B.E., Mr. I. Henry Burkill, Prof. E. O. Callen, Chemical Society, Dr. S. E. Chandler, O.B.E., Dr. L. Chalk, Mr. K. O. Emery, Prof. Ronald Good, Mr. W. Balfour Gourlay, Mr. F. C. Grigg, Dr. R. Gurney, Dame Helen Gwynne-Vaughan,

G.B.E., S./Ldr. A. E. Haarer, Mrs. Vera Higgins, Mr. J. Insch, Dr. Warwick James, O.B.E., Sir Murdoch McLeod, Bt., Mr. A. Mayfield, Mr. Richard Morse, Prof. T. G. B. Osborn, Dr. R. Pichi-Sermolli, Mr. W. R. Price, Mr. A. W. Rymer Roberts, Royal Horticultural Society, Prof. James Small, Mr. D. J. Scourfield, I.S.O., Colonel F. C. Stern, O.B.E., Dr. J. K. Spearing, Mr. W. H. T. Tams, Mr. Iain M. C. Talman, Dr. T. W. Wallis, Mr. R. Winckworth, Mr. H. A. Wootton, Mrs. Menie Watt.

The President called special attention to the donation of one hundred guineas to the Library Restoration Fund from the Royal Horticultural Society.

The following Fellows signed the Obligation in the Roll and Charter Book and were Admitted Fellows :—The Hon. Andrew Nicolas Armstrong Vanneck, M.C., and Miss Mabel B. Whitaker, B.Sc.

The President reported the death of Professor Johan Hjort, Foreign Member of the Society.

The following communications were read and discussed :—

Prof. J. McLEAN THOMPSON. A Contribution to our knowledge of the African Apocynaceae, with special reference to *Pleiocarpa mutica* Benth. (Discussed by the President, Professor F. E. Weiss, Mr. I. H. Burkill, Dr. C. R. Metcalfe and Dr. S. E. Chandler, O.B.E.) [Printed in full below.]

Dr. A. J. MARSHALL, Beit Memorial Research Fellow. Pre-gestational Changes in the Giant Fruit Bat (*Pteropus giganteus*), with special reference to an asymmetric endometrial reaction. (Discussed by the President, Professor E. C. Amoroso, Dr. Edward Hindle and Professor W. J. Hamilton ; Mr. Marshall replied.) [Printed in full, p. 26.]

The following papers were read in title :—

'Mollusca III.—Slugs (Testacellidae, Arionidae, Limacidae).' By Dr. H. E. QUICK. (Synopsis of the British Fauna, No. 8.) (Communicated by D. M. Reid, F.L.S.)

'Mexican and Central American Garter Snakes (*Thamnophis*) in the British Museum of Natural History.' By HOBART M. SMITH, C. WILLIAM NIXON and PHILLIP W. SMITH. (Communicated by H. W. Parker, F.L.S.) [To be printed in the *Journal, Zoology*.]

A CONTRIBUTION TO OUR KNOWLEDGE OF THE APOCYNACEAE WITH SPECIAL REFERENCE TO PLEIOCARPA MUTICA BENTH.

By J. McLEAN THOMPSON,
The Hartley Botanical Laboratories,
The University of Liverpool.

(With 18 Text-figures.)

Although the discovery of Apocynaceous plants has marched apace since 1888, little is known of the ways of growth and differentiation of the larger species or of how their flowering modes may come to be defined. In these respects, the need of detailed information has long been felt by those concerned with the

shrubby and tree-like Apocynaceae of Africa which have shown, so far, great constancy of specific floral structure throughout their many fruitful years but may be subject to progressive change of flowering habit, as age advances, and thereby have become a cause of some surprise.

It is the purpose of these pages to lift the veil of mystery from a single species in which such changes are pronounced and thus to form a background against which the habits of some kindred species may, in part, be judged.

Pleiocarpa mutica Benth. is a shrub of Tropical West Africa, which may attain tree-stature, and which was first described in Hooker's *Icones Plantarum*, Series 3, Vol. 2 (1876). Among the features noted, and which need be mentioned here, were its opposite, oblong, coriaceous leaves, with almost sessile inflorescences in the axils of some of them; and elsewhere, its inflorescences in nodal clusters, presumably upon maturing shoots. The presentation of the plant was naturally objective, giving no inkling as to Bentham's views on how the nodal clusters might arise through differential growth.

In several ways, his prior statements on the Apocynaceae touched more obviously the matters now in hand (Bentham & Hooker's *Genera Plantarum*, Vol. 2, 1874). For they stressed the frequency and variations of cymose flowering within this strange alliance, and noted how the inflorescences may be solely terminal, or single in the axils of paired or opposite leaves, or may be axillary to the most distal expanding leaves alone or to those most closely beneath them, and also how—in greater contrast—the clustered cymes of *Pleiocarpa* may be abundantly on knot-like swellings above the scars of fallen leaves.

It will be shown below how closely is this latter feature bound with cymose flowering and how this state of flowering is long maintained upon the species now in mind so that, in course of time, its slender shoots, its thickened branches, and its sturdy bole alike may play their parts in oft-repeated blossoming.

For present purposes, it will suffice to note that, as our knowledge of the Apocynaceae has grown, the actual positions of inflorescences on distal shoots have frequently been used as features of generic rank. This is well shown by Stapf's description of the Order in Thiselton-Dyer's *Flora of Tropical Africa*, Vol. 4, Section 1 (1904), in which the generic key described the inflorescences of *Pleiocarpa* as axillary, and rarely pseudo-terminal, and those of *Hunteria* as terminal or pseudo-axillary. To some extent, the flowering modes of these and other Apocynaceous plants were made more varied than is here suggested when the salient features of the genera and their species were described. Thus while *Polyadoa umbellata* Stapf was remarked upon for its flowers in terminal or pseudo-terminal clusters or in congested umbelliform cymes, at least six species of *Pleiocarpa* were said to flower in some profusion above their old leaf-scars. More recently, a liberty in flowering mode has been recorded for two further species of *Pleiocarpa*, thus causing growing curiosity as to what it may denote (Hutchinson & Dalziel's *Flora of West Tropical Africa*, Vol. 2, Part 1, 1903).

Initially, one's interest was aroused by Mr. A. D. Cotton who had remarked the widespread and prolific flowering of *Pleiocarpa mutica* and who thought its cauliflory worthy of exact enquiry. Throughout the somewhat lengthy study which this species has required, much valued aid came from the Gardens of Kew, Wisley and Edinburgh. And when it was at last apparent that the full flowering cycle would be hard to trace, by measured steps, through cultivated plants alone, materials despatched from Africa went far to settle many points which had remained in doubt.

Some comments on the habit of this plant may well explain why information on its ways of growth and differentiation is required.

Quite commonly, there is a point of major branching on the stumpy bole, at no great distance from the surface of the soil. The lateral shoots around this point may number three or four but are, more often, twin and opposite, and always distally diverging. They may approximate the central shoot in length and may be as sturdy as it in at least their basal parts.

In well-grown plants, the central and lateral shoots alike bear steeply ascending lateral branches at very varied levels, most often separated from each other by several internodes and nodes. Most of the secondary branches are long and sturdy and, in their turn, bear other major shoots from each of which may come, in time, still further sturdy shoots. Thus when all major branches are strongly grown, their slender distal leafy twigs may organize a common canopy.

A brief inspection of the distal twigs throughout a flowerless season will show that leaves may be retained upon the maturing lengths of shoot and that the downward passage to the older internodes and nodes is marked abruptly by nodal swellings, most often opposite, and sometimes single, and even ternate or quaternate. Although leaf-scars are evident beneath the minor swellings, dissection of the thicker nodes may be required to prove their constant presence. A like inspection of much younger plants at early stages in their first flowering seasons will rarely fail to show the distal twigs alone in lateral axillary flowering, and with the downward limits for expanding cymes fixed by the axil of the lowest leaves retained.

To follow downwards on the distal shoots of well-grown plants in any flowerless season is to note how steadily the nodal swellings increase in breadth and prominence and also change in aspect until they may be reckoned rugged wens upon the thickened branches, and even on the bole.

Some of the larger wens around mid-levels on the sturdy branches may carry few or single slender horizontal foliar shoots which are more often short than long and prove, most commonly, to be of intermittent growth. The wens involved bear constant witness to their prior flowering in that their main upturned faces are roughened by the short and crowded stumps of fallen inflorescences. Some of these stumps may be quite deeply chambered in the wens, while others are protruding. As to the left in figs. 1 and 2, the insertions of the shoots are often towards the lower margins of the wens where stumps of any kind are never found and roughened surfaces are mainly due to crumpled cork. These wens cause disappointment in the flowering seasons in that, at most, their flower-formation is uncertain and restrained. Apart from them, the long basipetal succession from minor nodal swellings on upper leafless lengths of shoot to rugged wens on greatly thickened nodes below will mainly show a power of seasonal flowering, increasing year by year, and even in a single season far surpassing that displayed at any time in the leaf-axils of the distal twigs. Thus, though a sturdy plant may come to flower in any season at all its nodes from mid-levels on its twigs to low positions on its bole, its distal flowering is but slight compared with that in progress far below.

Some further features call for brief comment since they are shown often by sturdy plants of very different ages. The first is illustrated by fig. 2 in which a single thickened lateral shoot, in course of basal flowering, rises quite steeply from a broadened node and has a well-defined and rugged wen beneath it. Although the dissection of such wens gives often proof of prior and repeated flowering, it rarely shows them to be bearing forming foliar shoots or stumps of others now discarded. Few of them show increase in size or flower again once basal flowering is in course upon the lateral shoots above them. Most commonly, the bases of these shoots are soon deformed by almost confluent flowering wens, while each opposing nodal wen without a sturdy lateral branch above it may show, as in this figure, signs of failing flowering in that a slender horizontal shoot is carried on its lower margin.

The main lateral shoots are often single—as above described—wherever nodal wens are opposite, but may be found in lineal pairs or in descending rows of three or more, and with a single major wen beneath each row, when ternate groupings of the wens is shown at the subjacent node. On sturdy plants, and from mid-levels upwards, main lateral branches are somewhat rare at nodes whose large and sturdy wens are grouped quaternately. But if these branches have been formed and the wens beneath them have persisted in active flowering, in course of time, the branches may be shed and leave persistent scars which are most obvious in the flowerless seasons, as to the right in fig. 3.

And finally, some common and related features may affect the distal twigs and younger lengths of shoot of all main branches, once nodal flowering has become progressively intensive at lower and still lower levels. For then, there comes a time for each such branch when, as growth in length may be renewed, its apical bud contributes but a single lengthened internode, and expanding



FIG. 1.



FIG. 2.

leaves are shed immediately from the obvious node above. No further internodal lengthening may then ensue; and soon the shoot-tip may be bulbous and may carry, from the leaf-scars upwards, nothing more than tiny and closely-crowded lateral scale-leaves, each with a single axillary bud. And when, at last, the phase of active body-growth is passed and flowering is resumed along the subjacent lengths of leafless thickened shoot, the axillary buds upon the bulbous shoot-tips, now in mind, may blossom once for all, or may at first be dormant and then flower freely in a later season. These minor terminal shoots are rarely shed when their brief flowering has ended, but rather die and shrivel so that their stark and spindly lengths are often obvious within the leafy canopies of large and shrubby plants (fig. 4). Such leafless shoots may also be replacements for main lateral branches at levels lower than the canopies, but then have commonly from two to several lengthened internodes beneath their bulbous tips. Their axillary origin is always evident until their parent nodes mature, and they ascend as steeply as the main lateral branches at lower levels. Whereas the latter's basal internodes remain extremely short and

later add but little to their lengths, the basal internodes of all these flowering shoots are quickly and completely lengthened, so that the shoots appear to be precociously developed. It may be noted also that early primary flowering is extremely rare at the nodal bases of the terminal and lateral minor flowering shoots alike and that, instead, these bases are the common sites of active lateral branch-formation. The lateral branches formed immediately beneath the minor distal shoots are often greatly lengthened and in full leaf long before the latter's bulbous tips are in open flowering so that it may appear, in later life, that flowering has proceeded in the forkings of main branches. The short and shrunken remnants of the minor lateral flowering shoots may often be observed on old and thickened nodes, with sturdy freely branching foliar shoots in lineal groups beneath them.

Nothing is known as to the course of growth and mode of branching whereby this plant may come to have the form and stature of a tree or as to possible



FIG. 3.



FIG. 4.

alterations of its flowering habits when it has ceased to be a shrub. But though no mention has been made above on many of its finer features with which systematists are concerned, it will perhaps be clear that some, at least, of those now stressed must be related specially to steps in differential growth.

In turning then to trace some steps of growth and differentiation which touch the matters now in hand, one should direct attention first to features of the lengthening shoots.

Increase in length of the main branches of a shrubby *Pleiocarpa* is rarely limited to one special season but may recur throughout each single year. The increments of current shoot are of most varied sizes but, as they cease to lengthen, their apical buds are always hidden in recesses each of which is, in the main, defined by the paired petioles of the last expanded leaves. The long extended internodes below are often few and have their upper limits marked by narrow nodes with large and opposite leaves, arranged most frequently in alternating pairs. There may be also large and single or ternate or quaternate leaves in close succession on the lower lengths of current shoot, and the bases of the increments may comprise a few unlengthened internodes and carry only tiny

chaffy scales upon the nodes between. Subtended and protruding buds are rarely obvious at any level until the fully lengthened internodes are quite matured; and even then, one may observe no more than single buds within the axils of the larger middle leaves alone.

There is no need to wait, however, until the lengthened internodes mature to form a fair picture of the current shoots. Thus, if a leaf-bearing node around mid-level on a tender shoot is sectioned longitudinally, the axillary buds disclosed will not be single but will be seen in lineal descending rows of two or three or more, and with the youngest basal (fig. 5). Beneath the latter will be always found a minute axillary meristem; and this despite much variation in bud-number within the axils of opposing leaves. To section nodes like this in all directions is to prove that the axillary chambers are closed laterally and that their greatest depth is shown when each bud-row and meristem below are seen as one unbroken series. To section also and compare the corresponding nodes on current shoots of varied ages is to show still further that the axillary chambers are at first extremely shallow and carry then no more than single buds,



FIG. 5.

with single meristems below, and quite adaxially upon their floors; that bud-formation is, mean time, the function of the meristems themselves; and that the chambers often deepen as the rows of buds are lengthened. In view of which, it will perhaps be evident that the single protruded buds observed around mid-levels on the current shoots are but the oldest and the highest members of axillary bud-successions. And further, it may be realized how long is the span of active life which some axillary meristems enjoy since one may find them still in course of bud-formation in deepened chambers within the leafless nodes on thickened lengths of shoots below. In sturdy plants, it is by no means rare to find from six to eight buds in a lineal row above a living meristem, and each still in a state of rest within the lengthened chamber.

As to the distal portions and the bases of the extended current shoots, it may be noted that if, perchance, four or five buds are in a row within the axil of a middle leaf, most of the upper leaves are found subtending only rows of two; and with the buds of lowering stature in more shallow chambers the higher one ascends; but always with a meristem beneath the row of buds. The buds within the axils of the basal scales may number only two or one, are most often

in retard, and are invariably in very tiny chambers with meristematic floors. In passing upwards from the basal scales to the most distal leaves, one cannot fail to note that only large expanded leaves have deep axillary chambers and that the longer is the row of buds per axil, the deeper is the chamber.

The course of flowering on this plant will be better understood if the salient features of its resting apical buds are also mentioned briefly. These buds are always short and wholly glabrous and never carry large protecting scales. They are, however, invested by a weft of slender living glands borne adaxially on the bases of the pair of large and distal leaves, much as in fig. 6, in which the glands are shown in solid black, the apical bud and leaves upon it are lettered M and L, and AB, AB are the most obvious and sturdy buds within the axils of the expanded leaves. The bud-leaves are in alternating pairs and rarely number more than six or eight in all. The present interest which the resting buds arouse springs, however, from three facts, repeatedly confirmed ; the first, that every bud-leaf retains an axillary fragment of initial meristem of purely apical



FIG. 6.

origin ; the second, that these meristems do not embark on axillary bud-formation until new current apical shoots are lengthening ; and the third, that not a single forming axillary bud is found upon this plant without a meristem beneath it. But since it is beyond one's purpose to trace the course of branching, it need be stated merely that, as a new increment of shoot is formed from any resting bud, most of the latter's primary leaves mature as basal scales ; that large expanding leaves come later from its rising apex ; and that the subtended buds close beneath the resting apical buds most commonly originate main lateral foliar shoots. And since also the flowering of *Pleiocarpa* is solely at the nodes of lengthened shoots and shows basipetal increase, it must be asked if a long continued bud-formation above axillary meristems upon the narrow floors of nodal chambers may in itself explain the present state of cauliflory. To seek an answer, one must now observe the features common to the highest leaf-retaining nodes on shoot-lengths which are little more than one year old.

It is convenient to choose for first comment the distal node of a very short shoot-length by which a branch had recently been extended. This choice is

made because the axillary buds are often few, the topmost one may be in course of lengthening as a leafy shoot, and since also the axillary chambers are rarely deep despite their floors of meristem. A node like this, selected in a flowerless season, is partly shown in fig. 7, as in mid-longitudinal section. A petiole, with shrunken basal glands, is to the left; and three buds in close and simple lineal succession are on the axillary chamber's inner wall. The basal bud might well be reckoned part and parcel of the meristematic floor but for its form and eminence. The large and distal bud is cut obliquely; and thus its apex and full foliation are not disclosed. Its upper leaf, traversed in full length, is from a middle node and has developing adaxial glands upon its base. This forming shoot is clearly foliar in nature since only leafy shoots bear glands like these on any of their middle or their upper leaves in plants of *Pleiocarpa*.

The shoots which spring thus from the topmost buds are often greatly lengthened in a single season; and yet the leaves subtending them may show no sign of falling for at least a further year. The rapid growth of the lateral



FIG. 7.

shoots need not involve the arrest of younger sister buds below or put an end to bud-initiation on the chamber floors. The younger buds are often found undamaged after the subtending leaves have fallen; and even later, there may be new bud-initiation on the chamber floors. And further, it has proved repeatedly that, though the bases of the lateral branches are in their second year of growth, from three to five axillary buds in close and simple lineal rows are on the inner walls of the narrow axillary chambers immediately below. Most regularly, these buds are forming cymes whose tiny lower scale-leaves alone may have adaxial basal glands. They often come to open flowering in basipetal succession when the nodes are four years old, and mainly leave short and persistent stumps upon the chamber walls. It seems that, with the sealing of the stumps, a change of function is imposed upon each chamber's meristematic floor since further bud-initiation from it has been sought in vain at many lower nodes from five to six years old. Thus though the open flowering of primary buds in simple longitudinal rows is delayed commonly in *Pleiocarpa*

until it is a factor in the cauliflory of the upper lengths of leafless shoot, it cannot by itself explain the rhythmic flowering of the sturdy nodes below or why this flowering is intensified the lower one descends. To seek a fuller explanation, one must hold in mind that flowering is intense and closely clustered at many low and greatly thickened nodes which give no sign of prior lateral branching ;

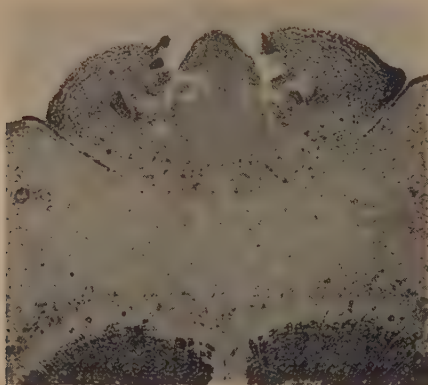


FIG. 8.

that many young and branchless leafy nodes bear only rows of cymes ; and that, quite commonly, the upmost cymes have fully flowered before the subtending leaves are shed. But though these upmost cymes are far removed from those in major clusters on the ageing nodes, they will appear on evidence to be the casual factors in the present state of cauliflory.



FIG. 9.



FIG. 10.

When a bud-row is long although its node is young, a transverse section may show the topmost bud in an early stage of cyme-formation (fig. 8). The basal 'leaves' are always to right and left, as is now shown, and adaxial glands are well-developed on them alone. More than a single bud in any row may be, of course, enlarged and, like the one now sectioned, quite unchambered, so that

the true entrance to the axillary chamber is only met and passed at the lower levels of the leaf-insertion. And since the chamber may be deep and has the younger buds in row upon its inner wall, a transverse section at low level may cross the leaf-trace and a young bud within the narrow chamber (fig. 9). Beyond the bud, there will always be observed the remnants of the subtending leaf's adaxial glands; and once again, the bud's first 'leaves' will be exactly lateral. The chamber narrows rapidly as one descends so that its floor is always seen in transverse section as a tiny mass of meristem, with curved trace beyond it (fig. 10).

When the node is young and its bud-rows are short, a longitudinal section may show the topmost bud in any row to be advanced in cyme-formation (fig. 11). The largest of its 'leaves' now sectioned may seem quite basal but are, in fact, the second lowest pair which strictly alternate with lateral ones like those exposed in figs. 8 and 9. Unlike their equivalents on the younger bud below, they have their tips quite suberised and have adaxial glands. The



FIG. 11.



FIG. 12.

figure shows the youngest bud to be unchambered, and that the axillary meristem is barely overshadowed by a petiolar fold.

These two examples must now serve to mark the contrast in the bud-conditions on the branches as a whole, and which may be quite evident at even neighbouring nodes. It does not seem, however, to have a bearing on the times of first flowering since topmost chambered or unchambered cymes may flower together at adjacent nodes. Apart from this, it is extremely rare for more than upper cymes in any row to flower and fade before the subtending leaves are shed, so that there is a major residue of forming cymes at any young and leafless node to play a part in cauliflory. In this respect, there is cause to think that when the bud-successions are long, and chambering is pronounced, the youngest cymes may not be brought to open flowering until the parent nodes are three or four years old. It need not be in doubt, however, that this cannot account in any way for the main flowering far below and that, for further information, one must examine now the younger nodes from which the leaves have fallen.

A young leafless node is shown partly in fig. 12, as in mid-longitudinal section. The topmost member of the bud-row is a fading cyme whose 'leaf-blades' have been suberised and are in course of shedding in the normal manner. There are three buds in row beneath the cyme, the lowest being the only one within a tiny meristematic chamber whose outer limit may be judged by an adaxial fold upon the leaf-stump. Some features of the stump require comment since they are of later consequence. Thus, the floor of the leaf-scar has an eccentric depression, always fixing the point of rupture of a cortical fibre-strand which is unaltered in later life beneath the lower surface of a flowering wen, although the leaf-trace strand above it may then be twisted and diffused. And further,



FIG. 13.

although the skin is suberised abaxially on the stump, as on the internode above, the adaxial skin twist leaf-scar and leaf-axil is unaltered and has the chambered axillary meristem within its bounds. If the illustration had been chosen from a node with chambered buds, the unaltered adaxial skin would be observed to stretch from the leaf-scar downwards to the meristem upon the chamber's floor. It is a point repeatedly confirmed that all but a narrow adaxial strip of petiolar skin is suberised before the absciss-layer is formed. Time and again this narrow strip of skin has been observed unaltered on nodes three years of age, and always with young buds and faded cymes close in line above it. Whereas in fig. 12 the unaltered skin runs horizontally, on the older nodes it runs obliquely downwards to the leaf-scar since its inclination has been altered,

step by step, as nodal growth has caused the leaf-stump's base to broaden. And since also this growth extends into the stump's adaxial face, the nodal chambers may at last appear as little more than small depressions high upon the steeply sloping strips of tender skin. The first interest which these narrow strips of skin arouse comes from the fact that they mark the only points upon the leafless nodes where skin is left unsuberised or hypodermal cork-formation is not in course. They are of present interest since they have been often found completely suberised on nodes from four to five years old which showed no sign of further bud-initiation and carried only remnants of their former cymes in rows.

It may be right to think that when these strips of skin are altered thus, the course of bud-initiation in simple lineal rows is fully run since cork is always found in place of meristem beneath the altered skin on nodes from six to seven years old. Quite evidently, this flowering phase must reach its close at very varied times and downward levels and, at the most, can leave on any node no more than simple lineal rows of scars or stumps to fully mark its progress. But since these stumps alone have proved, surprisingly, to be the prime source of clustered cyme-formation on old and greatly thickened nodes below, some features of the cymes themselves must be considered now in terms of their importance.

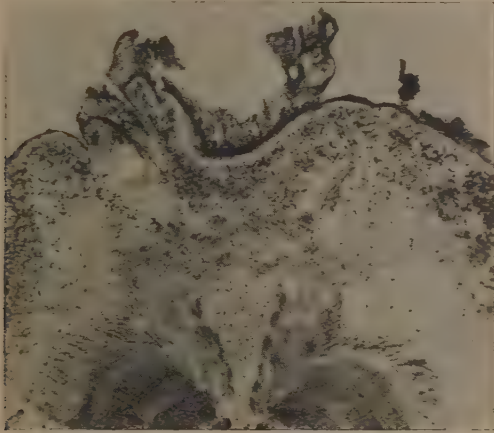


FIG. 14.

The axis of a young cyme of *Pleiocarpa*, within a row as now described, is short and stumpy and, as already noted, has the lowest of its pairs of alternating 'leaves' exactly lateral upon its base (fig. 8). The number of these pairs is inconstant, but commonly is five, and is rarely more than seven. A study of their development will show them always forming close beneath a small somatic apex and will prove that, as in a resting leafy bud, they come to carry in their axils nothing more than tiny fragments of axillary meristem of strictly apical origin. The first flower is initiated by the shoot-apex and comes to have the small and upmost pair of 'leaves', already formed, as its investment. The later flowers arise in a strictly basipetal succession which shows increasing lag in flower-development the lower one descends. These flowers are always single and axillary, each using to the full its parent meristem. At times, the downward course of flower bud-initiation is completed so that the smallest buds of all are in the axils of the basal 'leaves', to right and left. In this event, the

level at which the final absciss-layer is formed is beneath them so that the withered cyme can only leave a scar. By far more often, flower-initiation is discontinued at some low level on the shoot so that at last the basal 'leaves' to right and left retain residual meristems. In this event, the final absciss-layer is formed beneath the lowest flowers, and thus defines the length of stump which shall persist and, when the basal 'leaves' have fully fallen, may duly prove that



FIG. 15.

every meristem retained is still alive. To some extent, the features now in mind are shown in fig. 13 which represents an axillary row of buds in plan, and with the second in the cymose state. The topmost bud is shown as foliar, with single buds or buds in rows within the axils of its lower leaves. The circle RM represents the axillary meristem, with leaf-scar just below. The maturing cyme, 2, is shown as with five alternating pairs of 'leaves' and with five circles representing

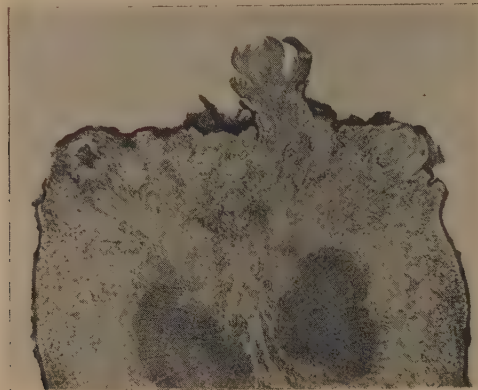


FIG. 16.

flowers. The two basal pairs of 'leaves' in solid black are well below the lowest flowers so that, with cymose flowering incomplete as here explained, at least the basal pair of 'leaves' are oft retained upon the stumps of faded cymes and duly furnish further cymes from their axillary meristems. It may be further clear that if cyme 2 bore flowers which numbered nine in all whereby

the flowering course was fully run, on fading, it could only leave a scar from which no later flowering could proceed.

It may then be plain that since the downward course of bud-initiation on the forming cymes is seldom run in full, at least the basal axillary meristems are



FIG. 17.



FIG. 18.

often quite undamaged upon the shortest stumps and, as the figure shows, may form, in time, new single buds which duly furnish further cymes upon the ageing nodes. These nodes in *Pleiocarpa* broaden greatly beneath the upper stumps which are, in consequence, much deformed and widened in their bases so that the single forming buds to right and left of them may seem engulfed, as seen in

transverse sections of a broadened node (fig. 14). The lower one descends in any row, the less the stumps are broadened or their bases widened, so that, as in fig. 15, a transverse section at low level often shows a ragged cork-clad stump quite central in a chamber, with large cyme-buds to right and left upon the chamber floor. And since the first full-grown cymes on any stump are very short, and since the nodes are always broadening as they grow, the stumps with basal meristems become engulfed or chambered and, in due course, give rise to further cymes in short close clusters round the parent stumps themselves. And since it is most often from the basal meristems on any stump that the first new cymes arise, still further stumps are added radially around each parent one until their clusters are confluent and a single wen is formed; and always with its surface greatly roughened by stumps both young and old (fig. 3).

Thus if a wen is sectioned early in a flowering season, new forming cymes may be observed to spring from it among short and closely crowded cork-clad stumps (fig. 16), while others, more expanded, may be basal lateral to those from which they sprang (fig. 17).

It is not known what is the span of life through which this oft-repeated cymose flowering may proceed. It is, however, certain that the span is long since, rhythmically, the sturdy shoots of long-established plants may still flower freely in the cauliflorous way along their greater lengths and have their basal nodes throughout in active and extensive blossom (fig. 18).

It will be clear that flowering in a *Pleiocarpa* is entirely primary, involving only young and superficial buds at each and every step. Accordingly, the cauliflorous state herein described contrasts in many ways with that dependent on endogeny (Proc. Linn. Soc. Lond. 156 Sess. Pt. 2. Dec. 1944). And since each step whereby the cauliflorous state of *Pleiocarpa* is maintained depends on uncompleted cymose flowering in its predecessor, like many members of its own alliance, this plant would blossom on its upper lengths of shoot alone if cymose flowering ran its course in full throughout each row of leaf-subtended buds (Proc. Linn. Soc. Lond. 157 Sess. Pt. 2. May 1946).

PRE-GESTATIONAL CHANGES IN THE GIANT FRUIT BAT (*PTEROPUS GIGANTEUS*), WITH SPECIAL REFERENCE TO AN ASYMMETRIC ENDOMETRIAL REACTION.

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(Communicated by Professor A. C. HARDY, F.R.S.)

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(Plate 2 and 8 text-figures.)

1. Introduction.

In a recent investigation of the breeding season of the uniparous fruit-bat of Ceylon, *Pteropus giganteus* Brünnich, it was observed that most of the uteri collected during the restricted conception period had one or other uterine horn appreciably swollen (fig. 1) before implantation had taken place (Marshall, 1948). Close examination revealed that while the single morula was still descending the Fallopian tube a considerable glandular modification had occurred at the end of the cornu below. The opposite horn retained its pre-fertilization dimensions; together they presented a striking asymmetry (fig. 2). Among 40 uteri which had accessory structures sufficiently intact to make correct orientation certain, the left-right pregnancy ratio was exactly 20-20.

The above phenomenon is difficult to fit into the generally accepted pattern of pre-gestational events in mammals. It would be expected that the activating hormones should flow from the active ovary into the blood-stream and become distributed equally to both horns of the uterus.

Once it was established that the ovaries and uterine horns of both sides were functional in *Pt. giganteus*, it was decided to try to investigate the problem with the material available. This consisted, unfortunately, of only the reproductive parts of bats collected and fixed in Bouin's fluid, 10 years previously. I am indebted to Dr. John R. Baker for his generous gift of the material, and to

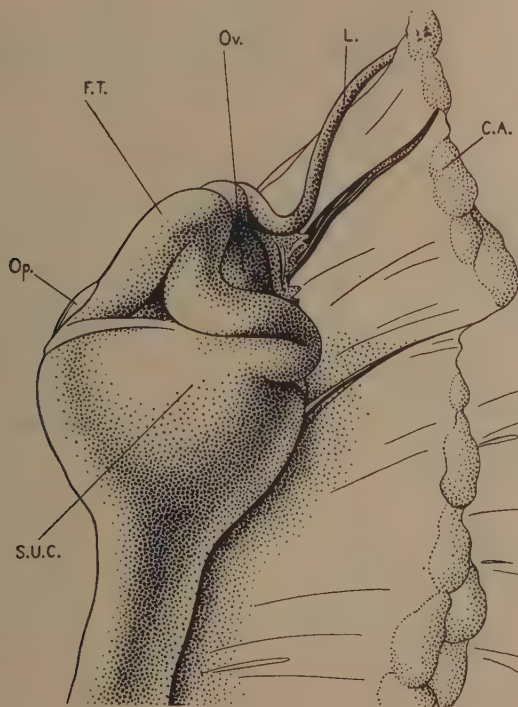


FIG. 1.—Asymmetric uterine cornu of *Pteropus giganteus*.
S.U.C. Swollen uterine cornu. Op. Opercula. F.T. Fallopian tube. Ov. Ovary.
L. Ligament. C.A. Corpora adiposa.

Mr. E. C. Fernando of the Colombo Museum who collected it originally on Dr. Baker's behalf. During the course of the investigation I have been fortunate in being able to discuss various of its aspects with Drs. J. R. Baker and O. L. Thomas and Dr. F. H. A. Marshall, F.R.S. has been kind enough to read the manuscript.

2. The anatomy of the female genitalia.

The vegetarian *Pt. giganteus*, or 'flying fox' of India, Burma and Ceylon is a big bright golden or reddish-brown bat, probably the largest known, attaining in the male a wing-span of 50 inches, and a body weight of $2\frac{1}{2}$ lb. The females weigh about half-a-pound less (Phillips, 1935). A criterion of

sexual maturity in the female is a forearm length of 170 mm. or more. The species has a sharply defined breeding season, copulating and conceiving in December–January, and giving birth approximately six months later.

Unlike some of the Microchiroptera (Matthews, 1941), the ovaries are identical, and each is densely packed with developing or degenerating follicles all the year round. Three incidental anatomical features are worthy of passing note:—

1. In the distal pole of the ovary, extending longitudinally through the investing fibrous tissue, one frequently finds blunt, blind pouches lined with ciliated epithelium. These have a thick fibrous wall. They generally do not exceed 600μ in diameter; but one, greatly swollen, measured 1,100 by $1,400\mu$ and extended from the distal pole right down to the germinal levels of the ovary (fig 3). These pouches are probably of mesonephric origin, and as in the case of the abnormal example just mentioned, may secrete and become enormously enlarged. This did not interfere with ovulation and luteinization.



FIG. 2.—Non-pregnant (No. 12) and modified uteri (Nos. 13–15) illustrating the asymmetric reaction. Letters A–D refer to uterine levels shown in figs. 6–9.

2. Throughout the female reproductive organs (and in the testis) there is an abundance of black pigmentation. In some uterine cornua a diffuse, though almost continuous layer runs in a half circle near the junction of the myometrium and the endometrium. The quantity and distribution varies with individuals and ages, but apparently not with season. In the ovaries individual pigment units may lie deep in the germinal tissue, for example, in the midst of developing oocytes, and in the Fallopian tubes pigmentation may occur densely in the walls as well as the connective tissue between the convoluted mucosa. There appears to be no systematic distribution from organ to organ. The most strikingly pigmented tube examined had its corresponding ovarian section completely free of pigment. Only small deposits were observed in bats which were almost certainly seven months old.

3. Fat always occurs in scattered deposits throughout the broad ligament and along the lines of condensed pelvic fascia and elsewhere. Among northern

mammals, Agduhr (1927) suggested that in the mouse comparable deposits might have a protective function, and Hansson (1947) found that in the mink even emaciated females still retained well-developed corpora adiposa.

The uterus in *Pteropus* is a primitive (Wood Jones, 1915) bicornuate structure in which the junction of the lumina does not correspond with the position of the fork as observed externally—the uterine body is strikingly septate within. The horns extend much further anteriorly than is usual in animals of similar size.

The ovaries are encapsuled. The capsule is oval and almost completely closed. It is protected and invested on one side by a fold of broad ligament and on the other by the mesosalpinx and Fallopian tube. The tube has an operculum at its opening to the peritoneal cavity and proceeds anteriorly exactly to the apex of the ovary, loops sharply in Ω -shape to the uterine level again and thence follows the uterine curvature before looping once more to discharge into the cornu (fig. 1). The course of the tube therefore is extremely simple. The mesosalpinx is separated from the ovary by an extensive closed

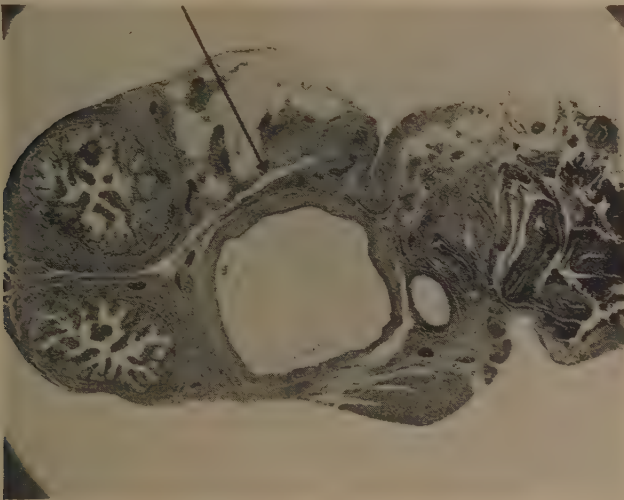


FIG. 3.—Transverse section, anterior pole of ovary showing Fallopian tube near top loop, the anterior limit of bursa (marked with arrow) and two abnormal, ciliated pouches.

bursa (fig. 4) which, constant in all ages and seasons, extends from the fimbriated operculum laterally on each side beyond the tube and anteriorly to a point past the apex of the ovary (fig. 3). At ovulation the egg is extruded directly into this bursa. The ovarian wall at this point becomes thin and has none of the large vessels obvious at its opposite pole. Thus the egg is shed into an almost completely closed pouch from which it can migrate directly into the fimbriated end of the tube without passing into the peritoneal cavity proper. At the same time a fluid exchange can probably take place between the peritoneal cavity and the bursa and oviduct.

3. The pre-gestational cycle.

The breeding season in *Pt. giganteus* is sudden in onset. There is only one breeding season a year, and all mature females in a given colony appear to become pregnant or contain sperms in the uterus or Fallopian tubes within a few days. Sperms were never found outside the period during which pregnancy

occurs. Copulation preceded ovulation in the eight females which were examined at a pre-ovulation stage. Sperms are readily observed packed densely with heads near the epithelium of the glands of both uteri. They appear as plentiful in the swollen horn as in the other, and penetrate into the furthest-most glandular recesses. They may occur in great numbers in the uteri of females whose ovaries as yet contain no egg which has differentiated to a stage where one can say that it will ovulate. Corpora lutea were found only in the months of pregnancy. *Pt. giganteus* therefore probably resembles the rabbit, ferret, cat, ground squirrel, mink (Hansson, 1947) and other mammals in which ovulation is conditioned by mating or erotic play between the sexes.

In *Pt. giganteus* the follicles are formed in successive waves of hundreds in which each individual egg is of approximately the same size as its neighbours. A few follicles of each clearly defined batch reach a size of approximately 220μ , with an ovum which reaches a constant 110μ ; in any given ovary two such



FIG. 4.—Transverse section ovary and bursa (to which arrow *A* points) at ovulation level. Black-staining material is blood, and immature corpus luteum is seen nearby. The egg came from the batch shown in top left-hand of the picture. Between the blood-clot and these lies the following crop (arrow *B*).

waves of follicles are generally seen. Thus we usually see about half the ovary (in all pre-gestational months observed) occupied by the comparatively few large survivors of one wave and the other half filled with primary oöcytes of the succeeding batch: the boundary line between the two being quite sharp. Although the September ovary is roughly half the size of that of December the same phenomenon is observed. As one lot of follicles becomes atretic the other matures. No extruded eggs, nor any follicles approaching the bursting size were observed except during the limited period during which sperms were found in the female tract. The vaginal epithelium was unfortunately too hardened to admit of a satisfactory examination in conjunction with the ovarian condition. The November juvenile ovary (forearm 150 mm., approximately seven months old) is full of young follicles apparently histologically similar to the primary oöcytes observed in adults.

Egg-formation continues throughout pregnancy although ovulation does not take place. In December one often sees half the ovary occupied by the developing corpus luteum and the remainder filled with follicles of two stages—a portion still occupied by atretic follicles of the generation which provided the fertilized egg, but the greater part filled with hundreds of primary follicles of the succeeding batch. That a spacial factor rather than any other inhibits egg-formation in the pregnant *Pteropus* is suggested by the fact that in May, the month of partus, one still finds odd maximal-sized eggs making their appearance in the rigidly limited stromal space between corpus luteum and fibrous ovarian wall. In one female two months pregnant, the ovary exhibited the customary two batches of follicles in the only corner not filled by corpus luteum. The significance of this continuous egg-formation after an embryo has started to develop may be that if abortion occurs—perhaps not infrequent in a flying, 'constantly bickering' (Ratcliffe, 1931) mammal such as *Pteropus*—another

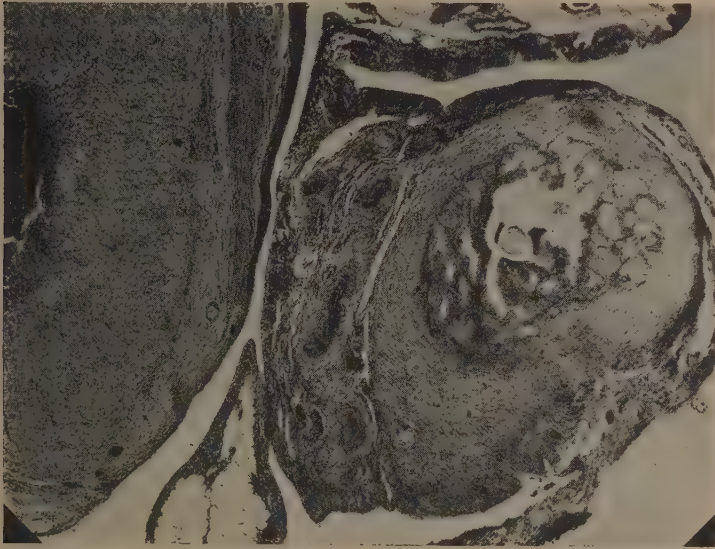


FIG. 5.—Tubal morula and corresponding developing corpus luteum with central blood-clot. Adjacent horns are in condition shown by No. 13, fig. 2.

ovulation and conception may take place very quickly. In the present species the epididymides contain great numbers of sperms throughout the year (Marshall, 1948); and in *Pt. geddiei* Baker and Baker (1936) report odd pregnancies occurring months later than the usual copulating season.

Both ovaries are functional at the same season. The ova developing in each appear histologically identical. Furthermore, an examination of the uterine arteries revealed the condition endarteritis obliterans in one horn (indicating a former pregnancy) and a recently implanted embryo in the other. Neither Baker and Baker, nor Ratcliffe, nor the present writer encountered twins, but Ratcliffe says that in an Australian species the fact of twins is 'definitely established... (but) very exceptional'. In no case during the present investigation were adjacent ovaries found with follicles maximally developed at the same time.

Luteinization follows sharply on ovulation. With a tubal egg (near the top loop) in the 4-celled stage, the corpus luteum measured $1,400\ \mu$ in diameter. With the morula in the 64-celled stage the corpus luteum measured $1,600\ \mu$, reaching maximal development before the fertilized egg reaches the uterus. Fig. 5 shows a tubal egg and the developing corpus luteum within the nearby ovary. The cleaving tubal egg always appears somewhat smaller in diameter than those measured in the follicles.

4. *The asymmetric endometrial reaction.*

The asymmetric endometrial reaction proceeds contemporaneously with luteinization. The December bats with appreciable swellings all had either a recently implanted foetus (one example), or a dividing egg in the tube or just below the tubo-uterine junction. There was always a corpus luteum. A big swelling did not mean implantation, but it was always accompanied by a big corpus luteum. December bats without the asymmetric endometrial development all had sperms in their tracts, but their follicles were yet intact and there was never a corpus luteum.



Fig. 6.—Section of swollen horn (point *A* on uterus No. 15 in fig. 2) at potential site of implantation. Arrow points to morula almost touching epithelium.

Fig. 2 shows the comparative development of the horns before and after fertilization. Fig. 6 (a section of the swollen horn at the level marked *A* on uterus No. 15 in fig. 2) shows the December horn at the site of implantation, including the morula close to the uterine epithelium. Fig. 7 shows the same horn at a slender level at a point *B* nearer the uterine fork and fig. 8 shows the opposite horn from that sectioned in fig. 6, i.e. at the level *C*, corresponding to the point at which implantation is about to take place in the potentially pregnant horn. The glands of both horns are active, but the activity of the restricted segment of endometrium where implantation will take place is extreme. In short, although an overall oestrous influence is activating the endometrium of the whole uterus, some special mechanism exists which makes development much more profound in a single limited region.

Fig. 9 (Plate 2) shows both horns sectioned at the point *D* (in fig. 2) in a mature November bat (No. 12) almost exactly a month before the date of conception.



FIG. 7.—Same horn as fig. 6, but sectioned further down towards the cervix at comparatively inactive part of the horn (point *B* in fig. 2).



FIG. 8.—Opposite (inactive) horn (point *C*) at a level corresponding to potential implantation site shown in fig. 6.

Fig. 10 (Plate 2) shows the undifferentiated horn of the juvenile nullipara aged seven months. Of the other uteri depicted in fig. 2, No. 13 had a tubal morula and No. 14, a recently implanted embryo.

It should be mentioned that even during the months when the asymmetric modification does not occur, bats sometimes exhibit slight disproportion right along the uterine cornu, but never to an extent even approaching that shown above.

Cleavage takes place during the passage of the fertilized egg down the tube so that by the time it reaches the uterus the morula has reached at least the 128-cell stage. Implantation is invariably within a few millimetres of the tubo-uterine junction. Although the uterine lumen is at its widest at this point, the morula never proceeds past the restricted area of modification.

5. Discussion.

It is suggested that the anterior and asymmetric uterine modification which ensures that a single implantation shall take place as far forward as is possible may be an adaptation to the arboreal and aerial habit of the animal. The female *Pt. giganteus* weighs up to 794 gms. (Phillips), and embryos may weigh (with placenta and preserved in Bouin's fluid) 118 gms. Fruit-bats spend a great part of their lives hanging upside down. It is instructive to compare this mode of life with, for example, that of the human female, where the foetus is supported by the anterior abdominal walls and the pelvic girdle. As the foetal weight increases and so changes the centre of gravity, the pregnant human female adopts a compensatory lordosis. In the fruit-bat the corresponding pressures are juxta-diaphragmatic, and the further towards this region the embryo is placed the less strain there is on the uterine ligaments and associated structures. It is possible too, that the anteriorly placed embryo may be associated with an adaptation towards the most efficient centre of gravity in flight.

Most bats produce one offspring at a time (Allen, 1939), but it must be mentioned that among some small insectivorous species, twins are customary and the American red bat (*Lasiurus borealis*) sometimes produces a litter of four (Lyon, 1903).

We come now to a consideration of the actual mechanism which prevents twinning and places the foetus as far forward as is anatomically possible. Apparently, twins do not often occur because, although there are often several large follicles in both ovaries, there are rarely or never two follicles simultaneously mature and ready for extrusion after copulation.

The asymmetric endometrial reaction occurs only after the follicle has burst and the ovum has passed into the peritoneal pouch described and a growth of luteal cells has appeared. It would seem then, that despite its asymmetry, the endometrial modification is due principally to progesterone. It would seem, however, that some other factor is involved—a mechanism which enables the progesterone to operate specifically on the glands of one restricted part of the uterine horn below the ovary which produced the egg and later the progesterone. In short, something (apart from the follicle hormone circulating in the bloodstream) causes progestational activities to be concentrated in one particular area making implantation elsewhere impossible. It is unlikely that the liquor folliculi which exudes at ovulation could act prodromally and directly on the endometrium of the cornu via the Fallopian tube.

A reflex nervous arc between the ovulating ovary and the adjacent uterus (causing vasodilatation and a resultant unequal distribution of progesterone) seemed a possibility. An attempt was made to investigate it so far as the material allowed. Although no sensory structure could be observed in the ovarian stroma, Holmes' axon technique (Holmes, 1947) revealed rich innervation of the uterine endometrium (fig. 11, Pl. 2) in the region of the swelling and further down the horn.

Many years ago various authors (Clivio, Hoogkamer, Gawronski, Kostlin, Acconci; cited by Stohr, 1928) claimed that they observed innervation of the

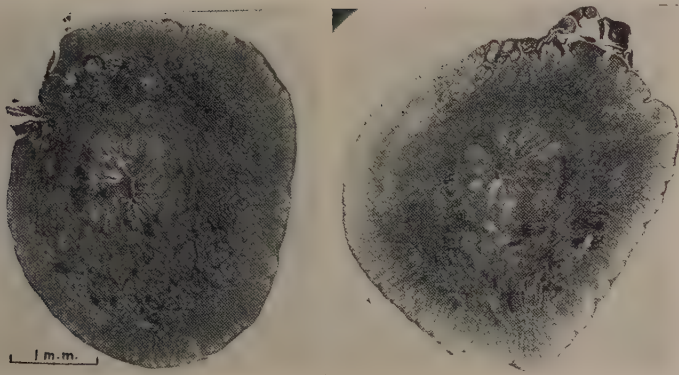


FIG. 9.—Both horns (at point *D*, No. 12 in fig. 2) of mature bat taken one month before conception period.

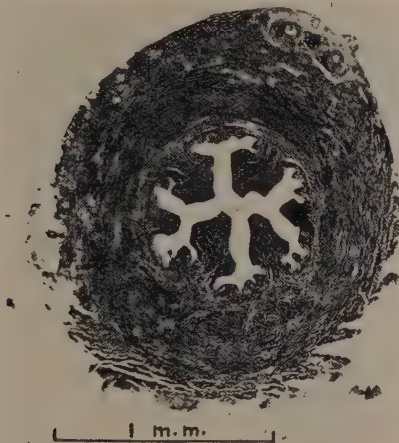


FIG. 10.—Inactive horn of juvenile nullipara.

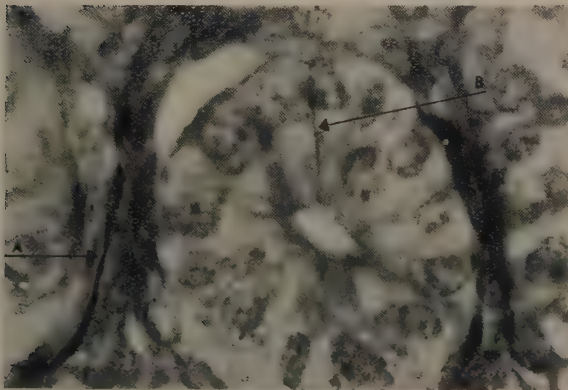


FIG. 11.—Endometrial glands of swollen horn and associated innervation ($\times 1260$).

Arrow *A* indicates nerve trunk and *B* an argyrophil intercellular structure.

(Figs. 3–10, iron haematoxylin at $10\ \mu$; fig. 9, Holmes' Axon technique at $15\ \mu$.)

endometrium, but in the intervening years their views appear to have been discredited (Stohr, Reynolds, 1941). It is a pleasure to pay tribute to my friend, Dr. William Holmes, whose technique made it possible to see nerves in the present material which had been preserved for so many years.

Fig. 11 (Pl. 2) shows also one of the curious silver-staining intercellular fibrils which occur irregularly in the individual glands in the swollen part of the horn. Whether there be terminal bars, secretory canaliculae or (unlikely) even possibly free nerve endings on the cells, cannot be determined with the present material. Until fresh material is available it is not possible to undertake collateral work with methylene blue either.

A widely quoted argument against the possibility of endometrial innervation is that in the Primates the whole decidua, with its nerves, would periodically disintegrate. Kolbrugge (1904, 1913), however, has claimed that a Javanese fruit-bat (*Xantharpha amplexicordata*) menstruates, though his description appears to refer to the discharge of mucus and leucocytes rather than to true endometrial sloughing. In *Pteropus giganteus* there is so far no evidence of sloughing of any kind. Hamlett (1934), on the other hand, contends that the insectivorous *Glossophaga* extravasates blood when its hypertrophied endometrium disintegrates after fertilization has failed to take place.

The present problem of asymmetric anterior progestational change may be allied to the general problem of the spacing of foetuses. In some mammals (bitch, sow, mink, rodents), depending on the type of uterus, the fertilized ova migrate considerable distances before implantation. In animals with a well developed corpus uteri, migration from one horn and implantation in the opposite has been recorded (Corner, 1921). Perhaps definite points of potential implantation such as that described in *Pteropus* have previously escaped notice because most mammals studied are multiparous, and so such glandular modification, if present, would appear more or less continuous along the uterine epithelium. Wimsatt and Wislocki (1947) have in American shrews described the establishment of epithelial crypts at implantation sites before nidation.

6. Summary.

1. In the bicornuate, uniparous fruit-bat (*Pteropus giganteus*) an asymmetric endometrial reaction occurs. Immediately following ovulation and while the morula is still descending the tube, the glands of the uterine horn adjacent to the ovulating ovary become strikingly modified. The opposite horn remains comparatively inactive.

2. The glandular activity occurs at the extreme tubal end of the cornu only and implantation always occurs there.

3. The possibility of nervous as well as humoral control of the endometrial reaction was investigated. No evidence of this was found in the ovary. Endometrial innervation is described.

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PROCEEDINGS OF THE GENERAL MEETING ON 9 December 1948

Professor G. R. DE BEER, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 25 November 1948, having been circulated, were taken as read and confirmed.

The President welcomed the President and Fellows of the Royal Entomological Society who had attended for the Joint-Discussion.

The following were thanked for gifts made to the Library since the last Meeting:—Miss Blanche Henrey, Mr. Dafydd Jenkins, Mr. R. S. Trickett, Prof. F. E. Weiss, the British Trust for Ornithology, Imperial Chemical Industries, and the Marine Biological Station, Ghardaqa.

The following Fellows signed the Obligation in the Roll and Charter Book and were admitted Fellows:—Dr. Elsie Burrows, Mrs. Agnes Margaret Hughes, Mr. George Donaldson Lockie and Professor Alastair Norman Worden.

The President reported the death of Miss Eleanor Vachell, Fellow of the Society.

A JOINT DISCUSSION WITH THE ROYAL ENTOMOLOGICAL SOCIETY on 'The Bearing of the parasite-host relationship on Taxonomy' was held.

The following speakers opened the Discussion—

Mr. G. H. E. HOPKINS, O.B.E. Some factors which have modified the phylogenetic relationship between parasite and host in the Mallophaga.

Dr. O. W. RICHARDS. Cuckoo Bees and Wasps.

Dr. J. RAMSBOTTOM, O.B.E. The parasite-host combination in plants, in relation to taxonomy.

The following took part in the ensuing discussion:—Dr. C. B. Williams, Pres.R.E.S., the President, Dr. S. C. Harland, Dr. W. H. Thorpe, Mr. A. J. Wilmott, Dr. W. B. Turrill, Dr. E. M. Delf, Dr. R. Melville, Dr. H. E. Hinton; and Mr. Hopkins, Dr. Richards and Dr. Ramsbottom replied to questions, [Printed in full below.]

Dr C. B. Williams, Pres.R.E.S., on behalf of the Royal Entomological Society, moved a vote of thanks to the Linnean Society for arranging the Joint-Discussion.

SOME FACTORS WHICH HAVE MODIFIED THE PHYLOGENETIC RELATIONSHIP BETWEEN PARASITE AND HOST IN THE MALLOPHAGA

By Mr. G. H. E. HOPKINS, O.B.E.

The Mallophaga are all obligatory parasites of mammals and birds. Unlike most other ectoparasites of these groups of hosts, which undergo some portion of their life-history away from the host, the Mallophaga spend their whole life on the host, which they never willingly leave so long as the host is alive. Their eggs are glued to the hair or feathers of the host, their young stages are all passed on the host, courtship and provision for the next generation all take place on the host, and on the death of the latter many of its Mallophaga grip a hair or a feather firmly with their mandibles and die in this position, so that even in death, host and parasite are not divided. This very close association with the host has freed the Mallophaga from the necessity of having a very high rate of reproduction to guard against the probability that any given individual will fail to find a suitable host, and it has also resulted in these parasites being very poorly equipped for transfer from one host to another except during actual contact of these latter. It follows that so many of the opportunities to transfer from one host to another that are available to Mallophaga are within the host-species and so few are extra-specific that there would be little to be gained by retaining the ability to live on a wide variety of hosts and instead the Mallophaga have become extremely narrowly specialized for life on a very limited choice of hosts and are perhaps the most specific of all ectoparasites. In many groups of Mallophaga it is the normal rule that every host-species has its own species or sub-species of louse, and in certain groups of hosts (the Procaviidae among mammals and the Tinamiformes among birds) it is sometimes even found that each subspecies of host is infested by a different species or subspecies of Mallophaga.

Turning to higher categories of the hosts, we find that almost every major division (nearly always the order and often the family) has at least, one characteristic group of lice peculiar to itself, so that if one is given a series of collections of Mallophaga from different groups of birds or mammals (but not labelled with the names of the hosts) it is normally possible to say with a high degree of accuracy from what group of birds or mammals each lot was obtained.

What seems to have happened is that both birds and mammals were infested by Mallophaga very soon after their divergence from the reptiles, that there was an initial period of very rapid evolution of the parasites in their new environment, and that subsequently their evolution slowed down until it proceeded almost in step with that of their hosts but normally somewhat more slowly and only very exceptionally (in the groups occurring on Procaviidae and Tinamiformes) more rapidly than that of the host. As I mentioned, it is normally possible to deduce the group of hosts from which a given batch of Mallophaga was obtained, and I now add that the lag in the evolution of the lice as compared with that of their hosts is often so considerable that their relationships remain clear while specialization has rendered those of their hosts obscure. It follows that, if the systematic position of a bird or mammal is in dispute, examination of its Mallophaga may provide very valuable evidence as to which view is correct. To take a well-known instance, ornithologists disagree as to the position of the

flamingos, some (perhaps the majority) considering them to be related to the storks while others hold them to be an offshoot of the ducks and geese ; I think all specialists on Mallophaga would agree that the latter view is the correct one. It is very significant that there does not seem to be any instance in which the opinion of mallophagologists as to the systematic position of a group of birds is at variance with that of the majority of ornithologists without the louse-students being able to claim the support of at least some workers on birds.

As is usually the case when any new discovery is made, there has been a certain amount of exaggeration of the value of the approach to host-relationships by way of those of their Mallophaga, and in particular, mistakes have been made owing to a lack of understanding of certain factors that we are only now beginning to appreciate and that must not be overlooked if our deductions are to rest on a sound foundation. Among these factors are discontinuous distribution, which I prefer to call secondary absence, secondary infestations, convergent or parallel evolution, and bad taxonomic work.

Among instances of secondary absence on a large scale are the absence of Mallophaga of the family Trichodectidae from pigs, seals and hyaenas, though they occur not only on all other families of the Ferungulata (that is Carnivora, Artiodactyla and Perissodactyla), but also on various other groups that diverged from the common stock before hoofed mammals and Carnivora had split off from one another, and the very peculiar fact that the genus *Falcolipeurus* occurs on many large birds of prey belonging to very different groups but not on any small ones, the latter instance being particularly interesting because it seems obvious that size has been the limiting factor though we do not know in what way it has worked. I think it difficult to over-estimate the possible importance of secondary absence in accounting for differences in the Mallophagan fauna of two different hosts. There is, for instance, one particular species of hyrax which possesses no less than eight different species of Mallophaga belonging to six different genera or subgenera, whereas there are other species of hyrax in which fairly adequate examination has only revealed two species of Mallophaga. Let us suppose that two different sets of descendants of the hyrax with eight lice were each to lose six of their lice, but a different six, and it becomes obvious that any deductions from the lack of relationship between the two pairs of survivors of the original set of eight lice would be extremely misleading. I am absolutely convinced that something very similar has happened many times and that we must not put any great weight on lack of resemblances between the Mallophaga of two different hosts.

Secondary infestations are well exemplified by the occurrence of a genus otherwise strictly confined to the petrels and their relatives on the skuas, which are gulls that have taken to obtaining food by buffeting other birds until they force them to disgorge ; the louse was doubtless acquired when some ancestral skua was robbing an ancestral petrel. Another good example is the occurrence of indistinguishable forms of *Felicola* on such distantly related hosts as the domestic cat, the civet and the white-tailed mongoose.

Examples of convergent or parallel evolution are less well-known and we owe most of our knowledge of them to Miss Clay. She finds that there are indications that development of a rather characteristic form of sclerotized clypeus that has been used as a generic character is perhaps correlated with feather-texture and may be of little or no significance in tracing the relationships of the Mallophaga that have this character, and also that certain stout-bodied forms found on pigeons, for example, that have been considered to be fairly closely allied to the rather similar Mallophaga of other groups of birds, are in reality so closely related to almost linear forms also found on pigeons that one form has certainly been derived at no very distant date (geologically speaking) from the other.

Perhaps the less said about bad systematic work the better, and I will only remark that the quality of much of the systematic work on Mallophaga is as bad as that of any to be found in biology—which is saying a very great deal.

Having mentioned the factors that limit the way in which we can use infestations with Mallophaga as evidence for the phylogeny of their hosts, it may be useful to examine under what conditions the lice can give us valuable pointers. We must be sure, first, that the resemblances between the Mallophaga we are comparing are genuine and not the result of bad systematic work, including under that term the mistake of allowing ourselves to be misled by characters that are the result of convergent or parallel evolution into suggesting louse-relationships that do not really exist. Next we must be sure that the mallophagan genera we use as evidence are representative of one another on the two groups of hosts, since without this condition the absence of resemblance between the lice of the two hosts may merely be due to secondary absence in both cases. And there must be sufficient instances of resemblance to exclude the likelihood that we are dealing with secondary infestations. I have suggested elsewhere that one correspondence between the lice of two hosts whose hypothetical relationship to one another is under examination means very little, that two such resemblances establish a probability that the relationship is genuine, and that three correspondences come very close to a certainty. Going back to the flamingos as an example, they are known to be infested by four genera of Mallophaga, of which one is found on both storks and Anatidae so cannot help us. The three other genera found on flamingos are all found on ducks but not on storks, and two of them are what I have called 'representative', in the sense that very closely related (but different) genera represent them on the storks. In this instance the evidence for a close relationship between the flamingos and the ducks to the exclusion of the storks is so strong that I think it conclusive. On the other hand, the fact that the genera found on the Musophagidae or plantain-eaters, usually placed with the cuckoos, do not include any cuckoo-genera of Mallophaga but do include two that are characteristic of the game-birds, are no more than highly suggestive, because these two genera may have begun to infest plantain-eaters merely because in the very distant past an ancestral plantain-eater used a dust-bath just after a game-bird, and acquired the lice as a result.

Finally I want to mention one anomaly for which I am quite unable to find a satisfactory explanation, in the hope that someone here may be able to suggest one. As I mentioned before, among the Procaviidae—hyraxes or conies of the rocks—it is very commonly the case that a subspecific difference in the hosts is accompanied by a specific difference in one of the Mallophaga infesting them, a representative of the genus *Procavicola*. In most of the areas occupied by *Procavia capensis coombi* and *Procavia capensis letabae* this holds good, *coombi* being infested by *Procavicola pretoriensis* and *letabae* by *Procavicola mokeetsi*. But in one area, adjacent to the range of *letabae*, *coombi* is infested, not by *pretoriensis* (as it ought to be according to our ideas) but by *mokeetsi*, the species characteristic of the other subspecies of host. This anomaly is so strange that I specially questioned the late Dr. Austin Roberts, an authority on the forms of *Procavia capensis*, as to whether there could have been any mistake about his determination of these specimens, but he assured me that they really were *coombi*. Can a mammal take on the physiological characteristics of another subspecies before acquiring its physical characteristics, and would this account for the observed facts? Frankly, I do not know, but that is the best hypothesis that has occurred to me, and if anybody present can suggest a better explanation I would be most interested to hear it.

THE EVOLUTION OF CUCKOO BEES AND WASPS

By Dr. O. W. RICHARDS.

Botanists often maintain, in my opinion with perfect propriety, that all plant-eating insects are parasites of the plants they feed on. From this point of view, a great deal of the taxonomy of insects might be regarded as a study of parasitism and indeed, there are very close analogies in the types of relationship one encounters. If, however, one considers only those insects which attack other animals, there are still at least three types of relationship which are commonly called parasitic:—

(1) The true parasites, e.g. lice. Host much larger than the parasite; effect of parasite on host slight; parasite characteristically degenerate.

(2) Parasitoids, e.g. Ichneumons. Host not much larger than the parasite; host normally killed before the parasite completes development; parasite not at all degenerate. These must be regarded essentially as refined predators.

(3) Cuckoo bees and wasps, e.g. *Psithyrus*. Host and parasite normally closely allied; parasite lives at the expense of the host's store of food rather than on the host itself; at least the female parasite with reduced food-collecting organs.

To-night, in order to limit the discussion, only the third category will be considered. It is almost confined to the Aculeate Hymenoptera, though analogies can be found in the Chalcidoidea and Cynipoidea and even in other orders of insects.

(a) The parasites are found in all stages from those which are difficult to distinguish from their host species to those which are now so distinct that the ancestral genus is uncertain. Examples:—*Vespa austriaca* (Pz.) is a parasite of *V. rufa* (L.); it lacks the worker caste but is otherwise a 'close' species. Amongst the bees, the female parasites are normally easy to distinguish from their hosts because the former lack pollen-collecting apparatus. The males of some species of *Stelis*, however, may be very close to the males of the host *Anthidium*. On the other hand, the numerous genera centering round the bee-genus *Nomada* form a complex group which has evidently long been parasitic. It is not possible in many of these genera to indicate an ancestral genus or even tribe.

(b) There is little doubt about the general lines of the evolution of these parasites, though many of the details are obscure. Amongst industrious species, there are many records of fights for nesting-sites, building-materials (e.g. resin), and food (e.g. insect-prey, honey). This is only natural where a number of individuals all construct their nests near one another at the same time of the year. There are several examples (ants, *Vespa*, *Bombus*) of industrious species which as an exception kill another individual of their own or an allied species and take over the nest as a going concern. This is very like what the cuckoo-species do, though with them a quarrel with the true nest-owner is often avoided and it is the host-larva or egg which is killed. To understand the problem fully, one would have to know the conditions which would lead to an industrious species becoming regularly parasitic; the degenerative changes would then almost certainly happen automatically. Twenty years ago, I suggested that the invasion of the territory of a northern, early-nesting species by an allied one with a more southern distribution would be one way in which such conditions could arise. I still think that this has been an important factor in temperate regions and Weyranch has found the idea applicable to the Vespinae. But there certainly must be other conditions which lead to the parasitic habit, particularly in the tropics. It is not surprising that, with an evolutionary mechanism of this type, parasitism should have been developed many times independently.

(c) The parasitic genera may be distinguished by three types of characters. Ancestral characters, resembling those of the host-genus; loss-characters, such as the absence of pollen-collecting apparatus in parasitic bees; and 'parasitic' characters which are certainly not ancestral yet do not seem to be directly related to the parasitic mode of life. Such characters are spinose developments of the thorax, and the development a conspicuous pattern, of either pigmented or pubescent spots. It is clear that there has been much convergence in the development of the parasitic characters. One example from the parasitic Vespinae may be described in detail. The common West European wasps fall into two groups differing conspicuously in the length of the malar space and in a number of other characters. *Vespula austriaca* Pz., with a short malar space, parasitizes the closely-allied *V. rufa* (L.), *Dolichovespula adulterina* (R. du Buyss.) and *D. omissa* (Bisch.) are closely-allied to and live in the nests of *D. saxonica* (Fab.) and *D. silvestris* (Scop.), respectively. Both groups of parasites share two important characters; the absence of a worker caste and the development of more strongly projecting clypeal lobes. Several ways of classifying these species are possible, but the most important divergence depends on how much weight is put on the parasitic habit and the characters associated with it. The morphological differences between the parasites and their hosts are not to-day of generic value. But it is quite possible that in a few million years there will be a tribe of parasitic Vespinae distinguished by the shape of the clypeus and the separate ancestry of the two groups may by then be obscured. One scheme of classification relies on what probably happened in the past, the other what probably will happen in the future.

(d) A number of parasitic genera attack several kinds of hosts, not all of which can be ancestral. Thus *Coelioxys* is allied to and usually attacks bees of the genus *Megachile*, but some species associate with *Anthophora* in a different subfamily. It seems that in these instances a species which has become firmly established as a parasite becomes less particular about its host so that transferences occur. Mr. G. E. J. Nixon gave me specimens of *Coelioxys rufescens* Lep. which were bred from the cells of *Anthophora furcata* (Pz.) and *Megachile* sp. which were nesting in the same log. This may be the way in which transferences occur in well-established parasites.

(e) It is usual for a parasitic species to attack several closely allied hosts. This has been specially studied in the bee *Nomada* which chiefly attacks members of the very large genus *Andrena*. In *N. panzeri* Lep., for instance, parasites with slight differences in colour-pattern can be recognized if series associated with each of the several *Andrena*-hosts are compared. It is not yet known whether these differences are genetic or whether they are due to differences in the conditions provided by the various host-species. On the one hand, such parasitic strains nearly grade over into the examples of very closely allied species associating with two close hosts. On the other, it is not altogether clear how such strains could become sufficiently isolated from one another to evolve into species. But perhaps the known tendency for strains to fly at different times of the year and to associate with discrete colonies of the hosts might suffice to allow sympatric evolution.

THE PARASITE-HOST COMBINATION IN PLANTS, IN RELATION TO TAXONOMY

By JOHN RAMSBOTTOM.

In the Plant Kingdom parasitism is found mainly among fungi, to a much less extent in flowering plants and algae, and in one genus, the tropical leaf-inhabiting *Strigula*, among lichens.

The best known parasitic algae occur among Florideae (Rhodophyceae). There are some borderline genera, but true parasitism probably exists where the alga is deeply anchored in the host, shows reduced vegetative characters, and there is a diminution in or absence of photosynthetic pigment. Such genera as *Harveyella*, *Choreocolax*, *Colacopsis*, *Stromatocarpus*, *Choreonema* and *Chaetolithon* show parasitism most clearly. They have completely lost the power of photosynthesis and in the last four genera the vegetative portions grow entirely within the host plant. Many semi-parasitic algae are restricted to a definite host, and in the true parasites host and parasite usually belong to the same order, often indeed to the same family*.

In Phaeophyceae there are a few parasites among the filamentous Ectocarpales. Here some reduced species of *Ectocarpus* are endophytic, others, such as *E. parasiticus*, definitely parastic, as are *Streblonema*, *Mikrosyphar*, and more particularly *Streblonemopsis*.

Parasitism and semi-parasitism are more common in Chlorophyceae. *Rhodochytrium* (Chlorococcales) occurs in leaves of Phanerogams and is related to endophytic forms which are apparently holophytic: it has been classed in fungi because it lacks chlorophyll, though it contains a red pigment. *Cephaeleuros* (Chaetophorales) is parastic on leaves, *C. virescens* causing the 'red rust of tea': its chlorophyll is masked by an orange-yellow pigment. *Phyllosiphon* and *Phytophysa* (Siphonales) cause gall-like swellings on leaves, but still retain their green colour.

Thus parasitic Green Algae seem to favour Flowering Plants as hosts in contrast to what is found in Red Algae.

Fungi are omnivorous in their tastes—for they attack all plant groups including fungi, and all animal groups.

Parasitic flowering plants are restricted to other flowering plants as their hosts. What has to be remembered is that the adoption of the parasitic habit in flowering plants is on a somewhat different footing than in all other groups of organisms except algae. There can be no doubt that parasites amongst flowering plants have arisen from what may be called normal plants, holophytic organisms able to provide themselves with the whole of the organic materials necessary for their existence. They have lost their chief physiological characteristic of photosynthesis and as a consequence of this the necessity for forming leaves; as they also obtain water and nutrient salts from the host plant, roots become atrophied or lost.

Intermediate hemiparasites occur, as in the Rhinanthoideae section of Scrophulariaceae represented in this country by *Melampyrum*, *Euphrasia*, *Bartsia*, *Pedicularis* and *Rhinanthus*. Here the roots form suckers which apply themselves to the roots of other plants. A similar habit is seen in *Thesium* (Santalaceae) a large genus with *Thesium humifusum* as its British representative. In these plants there is normal development of green leaves.

Other green-leaved hemiparasites are Loranthaceae with over 500 species—the seasonable *Viscum album* shows the general habit; Myzodendraceae, with about 10 species, parasitism here also being mostly of stems, the attachment usually a sucker.

The wholly parasitic plants in the British Flora are *Cuscuta*, *Orobanchae* and *Lathraea*. *Cuscuta* has the typical climbing habit of the Convolvulaceae: *Orobanchae* and *Lathraea* are root parasites. Orobanchaceae are closely allied to Gesneriaceae and might be regarded as a sub-order of it.

Balanophoraceae are wholly parasitic on tree roots, their tuberous rhizomes being attached by suckers: there are 15 genera and about 40 species. *Lophophytum*, a South American genus, has four species parasitic on roots of *Mimosa*;

*Setchell (1918) enumerated 51 parasitic Red Algae; 41 are parasitic on another member of the same family, 8 on other Red Algae not of the same family, and 2 on Brown Algae.

Helosis, also South American, has three species all parasitic on Myrtaceae; those of the other genera which are not monotypic are not restricted in their host.

Hydnoraceae, an African family with two genera and seven species, grow chiefly on *Euphorbia*. Lennoaceae, with three genera and five species, are South American herbaceous plants which are root parasites.

The most reduced in vegetative structure are the Rafflesiaceae: though the flower is normal the vegetative part is much like the mycelial strands of fungi. *R. Arnoldi* has a flower a yard across. *Rafflesia* (Malaya) has five species all parasitic on *Vitis* roots: *Pilostyles* (tropical America) eight species chiefly on Leguminosae: *Cytinus* (Africa) two species on *Cistus*.

How parasitism arose is a problem which has received no satisfactory explanation, though many have attempted one. It certainly originated more than once, for *Cuscuta* is Convolvulaceae, Orobanchaceae is most closely related to Gesneriaceae, Lennoaceae is in Ericales (in Engler's system), Loranthaceae, Myzodendraceae and Santalaceae (hemiparasites) and Balanophoraceae are Santalales, and Rafflesiaceae and Hydnoraceae in the next cohort, Aristolochiales. These last may have some close affinity, but it is probably rather in showing a tendency towards a parasitic habit than any phylogenetic connexion.

So far as host-parasite relation goes this is often not very close. Sometimes a species has a wide range of hosts (*Cuscuta* spp.); sometimes it is restricted to a single species (*Orobanche Hederae*). Some genera are restricted to a family (*Lophophyton*); some to a genus (*Rafflesia*). It is only when there is a definite relation between host genus and parasite that we can hope to gain a clue to the influence of the host on the evolution of the parasite. So far as I am aware no study has been made on these lines. Possibly some ideas could be gained from what occurs in fungi.

Fungi are regarded by many botanists as a decadent group because of their lack of chlorophyll, or, what is the same thing, their parasitism and saprophytism. However this may be there can be no doubt about their success as parasites.

The action of the parasite on the host may range from the apparently harmless to deadly. The problem as it is posed is whether this relation has had any effect on the taxonomy of the parasite and, alternatively, has it influenced the evolution of the host.

For our purpose we may first consider the matter as one of attack and defence. It does not profit a flowering plant to be parasitized by a fungus, and there are various structural and physiological characters which have been interpreted as defence mechanisms. These certainly serve as protections against attack, but they are so common and so varied that they cannot be interpreted as having been evolved for the purpose; such, for example, is cork.

Again, the generalized parasitism of many species is of no immediate interest in this discussion. It seems obvious that to find data for the possible effect of parasites on the evolution of hosts we have to consider those which are restricted in their host range, which often occur as epidemics, and which are of long duration.

One of the commonplaces of mycology is that when a species is grown in pure culture it almost always shows that it is a complex of strains. Further, that parasitic fungi—many of which it has not been possible so far to cultivate on laboratory media—show a similar complexity in constitution by being very restricted in their host relation. This phenomenon in parasitic fungi has been most studied in the Rusts. Strains of a species, morphologically indistinguishable, behave differently in their parasitism. They have been called biotypes, specialized races, biological species, etc., etc.

The occurrence of specialized parasitism was first recognized by Schroeter in 1879. It was Eriksson, however, who, in 1894, gave the first clear indication of the pathogenic differences between forms of the same species. In the well-known *Puccinia graminis* Eriksson by culture methods distinguished two

groups, *P. graminis* sensu stricto with its aecidia on barberry, and *P. Phleipratensis* of which the aecidia were unknown. *P. graminis* was then divided into six forms, *Agrostis*, *Airae*, *Avenae*, *Poae*, *Secalis*, and *Tritici*, according to the host plant to which they were restricted. *P. graminis* from *Agrostis* will not infect that from *Aira* and vice versa and so on through the list. Since then a great deal of research has been carried out.

To take only the one form, *P. graminis* f. *Tritici*, Stakman and Levine (1922) by using 12 species and varieties of *Triticum* separated 37 'physiologic forms', a number which has now been doubled. According to Stakman (1929) :—

'The constancy in the behaviour of the physiologic forms of *P. graminis tritici* is quite remarkable. There are, of course, fluctuations in the degree of infection, depending on the environmental conditions under which the rust develops. But these fluctuations are no greater than, possibly not so great as, those in the morphologic characters of fungi grown under different environment conditions. The determination of physiologic forms is quite as definite and precise as is the determination of morphologic species. The high degree of parasitic specificity of forms for species and varieties of higher plants also is noteworthy. Physiologic forms of the rust fungi are as definite and constant entities as are the species and varieties of host plants on which they grow.'

It should be pointed out that *Puccinia graminis* develops its aecidia on a few species of *Berberis* and *Mahonia*, while its uredospores and teleutospores occur on 98 species of 35 genera of Poaceae in North America alone. Presumably we should be safe in supposing that the species comprises at least a thousand specialized forms, strains, or whichever of the many terms is preferred.

The specialized forms of *P. graminis* are usually tested on pure lines of grasses. It has been shown, moreover, that the strains remain distinct on barberry and so are able to persist and multiply.

From the evidence we have it seems clear that the strains are constant except for occasional saltations; colour changes are not infrequent, but alterations in pathogenicity seem rare. It is probable that some of the strains may have arisen by hybridization between different forms. What is certain, however, is that a species like *Puccinia graminis* consists of a number of strains strictly confined even to pure lines in the host plants. The information we have is for the most part obtained from crop plants which have been sorted into pure lines. There is no reason, however, for believing that the phenomenon is restricted to parasites of hosts of economic importance. We may assume that *Puccinia graminis* was originally a species attacking a large number of grasses, and that it later became segregated into a series of specialized parasitic forms, or races, or, on the other hand, we may hold that it is these innumerable forms and races which constitute the species. On either view it seems clear that evolution of the fungus has proceeded *pari passu* with the production of new flowering plants, for otherwise, as there would be no new hosts, there could be no new parasitic strains.

Many Rust fungi exhibit the phenomenon of heteroecism, two different hosts being necessary for complete development: it is known elsewhere, among fungi only in two species of *Sclerotinia*. They also exhibit pleomorphism to a remarkable extent. There are four spore forms; uredospores, teleutospores*, aecidiospores, and spermatia or pycnidiospores. All species do not have the full quiver; there are a number which have only the teleutospore, or teleutospore and uredospore.

The most widely held opinion about the primitive forms is the unexpected one that the original Rusts were heteroecious and possessed all four spore forms: they were long-cycled (macrocyclic), and heteroecious. It is not possible to

* Teleutospores are really probasidia; on germination each cell produces a septate-basidium.

enter into the arguments for this, but all Rusts on Pteridophytes are long-cycled and heteroecious—of the 50 North American species on Coniferales, 47 are heteroecious, on the grasses all are heteroecious. Short-cycled (microcyclic) forms are almost unknown on the lower natural orders, whereas on the higher orders, they constitute about 45 per cent.

It is evident that the host has been a very important factor in the development of Rusts. The autoecious genus, *Phragmidium*, is confined to Rosaceae, many species occurring on *Rosa* itself: *Ravenelia*, with very few exceptions, is restricted to Leguminosae. In heteroecious forms more than 50 species of *Gymnosporangium* occur on Cupressineae in the teleutospore stage, and, with two or three exceptions, the alternate aecidium or *Roestelia* stage is on Pomaceae.

Another interesting point is that where a host genus appears to be undergoing change at the present time—the phraseology might be 'in an active state of evolution', or, alternatively, 'when they are difficult to define'—the parasitic rust seems to be behaving similarly, e.g. *Rosa*, *Rubus*, *Viola*, *Eupatorium*.

All microcyclic forms have been derived from macrocyclic forms. The close resemblance of the teleutospores of certain microcyclic species has been stressed since Dietel, in 1897, noted the similarity of the teleutospores of *Puccinia Mesneriana* on *Rhamnus* with those of *P. coronata* which has its aecidia on *Rhamnus*, and the same similarity between *P. ornata* on *Rumex* and *P. Phragmitis* on grass with its aecidia on *Rumex*. After about 15 pairs of such correspondences had been recorded, Tranzschel in 1904, used it for discovering the alternate host of the plum rust *Puccinia Pruni-spinosae*, which has teleutospores with the same characteristic markings on their walls and a similar shape to those of the short-cycled *P. fusca* on *Anemone*: by experiment he proved that an unattached aecidium on *Anemone* was the elusive second form. He announced what is now known as Tranzschel's law: the probable aecidial host of a heteroecious rust may be indicated by observing the host of a short-cycled rust with morphologically similar teleutospores.

Using the symbols A, U, T for aecidiospore, uredospore and teleutospore respectively.

Puccinia Pruni-spinosae has A on *Anemone*, U and T on Amygdalaceae and *P. fusca* has T on *Anemone*. But there are also *P. cohaesa* with A, U, T, all on *Anemone* and *P. tucsonensis* with A and T on *Anemone*, having the same characteristic teleutospores. Many similar relations have been worked out by American uredinologists*.

In one instance such teleutospores have a similar micro-chemical reaction: the stalks of those of *P. Pattersoniana* on *Agropyron* with aecidia on *Brodiaea*, and of *P. Moreniana* on *Brodiaea*, stain blue with iodine except just beneath the spore.

Another unexpected conclusion is that *Uromyces* with one-celled teleutospores has arisen from *Puccinia* with two-celled teleutospores. We find correlations between certain species of the two genera, both heteroecious and autoecious, as well as between heteroecious and microforms. As these occur on the same hosts there can be no doubt that they have evolved there.

In the interesting genus *Endophyllum* the teleutospores are borne in aecidia (or the aecidiospores germinate as teleutospores, if another view be taken). By applying the principle of correlation it is apparent that *Endophyllum* is a composite genus with species derived directly from the haploid generation of long-cycled forms. This has all taken place on the same host.

What about the effect on the host plants? So far as we know there is none. Parasitized plants are frequently hypertrophied and there is often a perennial

* J. C. Arthur (and others). *The Plant Rusts (Uredinales)* 1929. H. S. Jackson, Evolutionary tendencies in the Uredinales, *Mem. Torr. Bot. Club*, 18, 1931.

mycelium which overwinters in the rhizome or rootstock. Such plants are often so distinctive in appearance that they have been regarded as distinct species. But the effect is transitory. It is possible that in the ages some individuals have mutated as a result of the stimulation of a pervading parasite, but of this we have no evidence. Infection may be extensive and constant, but the host remains intrinsically the same.

Though Rusts give the clearest picture of evolution in relation to parasitism abundant evidence can be obtained from other groups.

How constant an infection may be is seen in the internal mycelium under the seed-coat of some species of *Lolium*, which is carried on from generation to generation. Here the parasite is kept under control. In spite of much sporadic research we have no clear indication of any effect of the fungus on the host.

Other forms of subjection, however, have resulted in what is known as symbiosis. This we find in Lichens where the union of fungus and alga is so close and the resulting structures so characteristic that they are classed as a separate group. The fungus constituent has been modified so much that if it is classed among the fungi it still requires separate treatment. It cannot be cultured in the usual way—indeed the fungus of no characteristic lichen has yet been cultured. It is assumed that the algal constituent has undergone no change. There is some evidence that it has—but lichens are not popular in the schools and their many fascinating problems receive little attention.

The internal yeasts of insects are apparently of genera and species unknown elsewhere. Their evolution must have proceeded along with that of the insects, and the view has been put forward for at least one group of insect, that its evolution was dependent on that of the internal symbiont.

Where the host has certainly altered and been affected in its evolution is the flowering plant saprophyte. All saprophytic flowering plants are symbiotic, and the vast majority of them have fungi as their so-called partners. I would go further and say that all saprophytism started as parasitism—cf. *Armillaria* and *Gastrodia*, and that it is not until the parasite is harnessed so that it gives as well as takes that the flowering plant is obviously affected in an evolutionary sense—and the path along which this compromise leads it, is shorn of the glory of photosynthesis. It might just as well have adopted the parasitic habit.

GENERAL DISCUSSION

Dr. C. B. WILLIAMS asked Mr. Hopkins if he could give further particulars on the occurrence of several species of Mallophaga on the *Hyrax* in East Africa, as the occurrence of several closely related species in a single ecological niche was of particular interest.

Dr. S. C. HARLAND said that he always felt that a flood of light could be thrown upon this kind of taxonomic question by even elementary knowledge of relevant genetics and cytology of the types concerned.

The only work he could recollect for the moment was published by Bacot in 1917. He made crosses between the head and body louse of man, and got fertile hybrids. He was, however, inclined to regard them as distinct species.

Dr. W. H. THORPE referred to Dr. Richard's conclusions that the typical cuckoo bee life history had been evolved through industrious individuals having developed a tendency to compete for half-made nests either of their own or later of closely allied species in order to use them as going concerns for their own purposes. This seemed to him of very considerable interest as evidence of long standing plasticity of behaviour; for it must involve the ability to take up the

routine of nest making at any one of a number of points and perhaps also to break off at one particular point and recommence at a new one. That the nest-making behaviour of the Bombidae is in many respects stereotyped is, of course, very well-known. If example were needed, there is the work of Plath (1938) who found that nest-making behaviour patterns offered valuable criteria for constructing a natural classification. It seems that the work Dr. Richards has described shows very clearly that besides this stereotyped behaviour, there must always have been great plasticity in the appetitive behaviour which links together the items of rigid instinctive behaviour in the strict sense. Dr. Thorpe pointed out that such plastic behaviour seems to be on a par with the very remarkable degree of plasticity recently revealed by the work of Baerends (1941) on the behaviour of *Ammophila*.

Secondly, Dr. Thorpe discussed the suggestion that in this group there is evidence of sympatric speciation. He said that he hoped Dr. Richards would enlarge upon this point because it is theoretically of such great interest and he would like to be certain that he had understood his suggestions aright. As he understood it, the argument was that during the initial stage of becoming parasitic, the species would be specialized to one particular host species. Then when it has reached the stage of being purely parasitic, it is in some way enabled thereby to become less specialized in its host requirements and to transfer its attentions to new hosts. Subsequently to this it is envisaged that new strains are developed, each attached to different hosts. It is thus supposed that the insect in the first stage is monophagous. It then becomes polyphagous with a tendency later, by again becoming monophagous, to split up into strains held, by some means at present not known, to different hosts. Thus there is apparently evidence of the existence of every transitional stage between closely related strains and distinct species.

Mr. A. J. WILMOTT said that he doubted whether the specificity of parasites was always as great as supposed. *Cuscuta epithymum*, so common on *Calluna* and *Ulex* on sandy commons, was not so long ago found attacking a large number of species—over 20 he thought—in a field near Wye in Kent. And some years ago at Weston-super-mare, on a wall between four and five feet high, covered on the inside by ivy for perhaps 50 yards, he found a large number—perhaps 200 or more—specimens of *Orobanchë*. Some were obviously *O. Hederae* with yellow stigmas and subglabrous corollas, but some had purple stigmas and were densely glandular. The latter could only be called *O. minor*. And there seemed to be gradations between them. This was apparently an example of two allied species occupying identical habitats.

Dr. W. B. TURRILL referred to parasite-host relationships in the genus *Orobanchë*. He remarked that there was some evidence of specialized strains in *O. apiculata* Wallr. (*O. minor* Sm.) and suggested that the problems concerned would form a suitable subject for investigation by methods of experimental taxonomy.

Dr. E. M. DELF said that she had enjoyed listening to the various contributions and was especially interested in the underlying features in the parasite-host relationship which might be common to both animals and plants.

The President had said that the amount of uric acid excreted by two similar kinds of tortoises had been proved to be very different and that some such metabolic or biochemical differences might account for their having a different selection of parasites. This suggested to her the question as to whether a parasite gained from the host some substance otherwise lacking, or whether there was absorption of some component making possible a new synthesis. In a short article in *Nature* (1945) Prof. Keilin claimed to have detected by

spectroscopic methods the presence of haemoglobin in nodules of leguminous plants, which exhibit symbiosis (i.e. a balanced parasitism) between certain bacteria and the plant in question. Haemoglobin had not hitherto been detected in the plant kingdom, and, according to Keilin, neither the tissues of the leguminous plant alone, nor a culture of the causative bacteria gave the reaction for haemoglobin.

If this be accepted, it may well be that the possibility of the synthesis of a new product may affect the question of the production and maintenance of new species in either parasite or host and may even throw light on genetic data if these become available.

Dr. H. E. HINTON : A discussion of parasitism usually begins, as has this one, by selecting a few special cases. The parasites and their hosts are listed. Attention is then drawn to some of the more spectacular structural features that have been evolved in this or that group of parasites, and the functional significance of a few of these morphological features are then described with varying degrees of success.

We may suppose, however, that when in a pair of species a host-parasite relationship is first established no obvious structural alterations appear immediately, but that a necessary pre-requisite for the invasion of the host by the parasite is an adjustment at a physiological level. It is usually only after there is a long history of parasitism that adaptations at a morphological level are noticeable. For this reason we are unlikely to get very far in understanding the development of a parasitic from a non-parasitic relationship by merely making lists or describing structural alterations of groups that have already had a long history of parasitism. It is more important to concentrate attention on fewer species and try to discover the exact conditions they require for existence in or on a particular host. As a matter of fact, there are remarkably few insects about which much is known from this point of view. For instance, one can say that the precise details of the nutritional requirements of only a dozen or so species are known. But from what is already known in these cases we may suspect that the descriptive and morphological approach to the problem is not very effective. As an example we may consider the moths of the genus *Ephestia*. Though these are not parasites in the ordinary sense of the word, there is no reason to believe that their physiological relations with their environment differ in principle from those between some parasites and their hosts.

There are three common species of *Ephestia* caterpillars that feed on stored products :—*E. kuehniella*, *E. elutella* and *E. cautella*. Their nutritional requirements have been studied by Fraenkel, Blewett and Busnel. *E. kuehniella* can develop successfully without riboflavin, and glucose or fructose are of no importance to it. The other two require appreciable amounts of riboflavin as well as glucose or fructose. The insensitivity of *kuehniella* to riboflavin accounts in large part for its success in infesting flour of high extraction, whereas the other two are unable to do so for lack of riboflavin even if their requirements of glucose or fructose are met. It should be noted that these caterpillars are so alike that it is only very recently that systematists have been able to distinguish between them on morphological characters.

Dr. R. MELVILLE, referring to the open question thrown out by Mr. Hopkins, recalled that sheep feeding on pastures growing on soils deficient in cobalt suffered from a disease called pining ; other stock on pastures where the soil was rich in molybdenum suffered from scouring as a result of ingesting an excess of this element. It was evident that the soil acting through their food, may have a profound effect upon the physiology of animals. This suggested a possible reason for the differentiation of the subspecies in *Hyrax* and their disjointed distribution. An investigation of the amount and identity of the

trace elements present in sample localities across the range of the species might yield valuable results. If the differentiation in *Hyrax* proved to be correlated with the trace element content of the soil of their habitats, then the resulting physiological differences in the host may be sufficient to account for the differentiation in the lice also.

Physiological differences between individuals of the host plant may govern the choice of host by an insect parasite. Thus, of two trees of the common oak under observation for several years, one always bore numerous marble galls caused by the gall wasp *Adleria kollari*, while the other only 20 yards distant remained free. There was a possibility here of genetical differences, if the oaks were slightly different segregates from the hybrid of our two native species, but this nevertheless implied a physiological difference. Recent work on stocks for fruit trees had shown that the effect of stocks on the scion was linked up with diverse capacities of the roots for accumulating particular trace elements. There was, accordingly, some reason to think that the parasite host relation could be modified by the effects of trace elements absorbed by plants.

Mr. HOPKINS replied that he had taken seven of the eight species of Trichodectidae off one individual host (*Hyrax*) and all eight off the same host-subspecies in the same locality. Also, that two of the species are so closely related that one cannot distinguish the females, while another four all belong to one genus and two of these four species are very closely related members of one subgenus, the third and fourth being subgenerically distinct from the first two and from each other.

PROCEEDINGS OF THE GENERAL MEETING ON 6 January 1949

Colonel F. C. STERN, O.B.E., M.C., Vice-President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 9 December 1948, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. R. B. Dawson, Miss C. M. Eardley, Dr. R. Melville, Mr. Richard Morse, Dr. M. H. Pirenne, Mr. W. R. Price, Dr. J. Ramsbottom, O.B.E., the Australian and New Zealand Association for the Advancement of Science, Adelaide, and the Zoological Society of London.

The Vice-President in the Chair, called attention to the donation of £25 from the Zoological Society of London to the Library Restoration Fund ; and a special vote of thanks was accorded.

The following Fellows signed the Obligation in the Roll and Charter Book and were admitted Fellows :—Mr. John Harrison Halliday and Mr. Edward Augustine Ellis.

The Vice-President in the Chair reported the deaths of Mr. William Borlase and the Rev. Henry Purefoy FitzGerald, M.B.E., J.P., Fellows of the Society.

The following communications were read and discussed :—

Miss R. GUINEY. On the whereabouts of the 'Oxford Copy' of Rudbeck's *Campi Elysi*. (Discussed by Mr. S. Savage, Mr. W. T. Stearn and Professor T. G. B. Osborn.) [Printed in full below.]

- Mr. E. A. C. L. E. SCHELPE. Mountain Vegetation in Southern Africa.
 [With Kodachrome cine film.] — (Discussed by Dr. T. T. Barnard and
 Colonel F. C. Stern, O.B.E., M.C.)

Abstract,—

The vegetation and its environment on the major mountain ranges in Southern Africa were discussed. South African species of the Proteaceae, Bruniaceae, Restionaceae and Ericaceae are plants requiring a moist temperate climate and show a marked preference for areas in which quartzitic rocks occur. The Cape South-western Region fulfills these requirements. It is inhabited by a great number of individuals of these species. Such close aggregation of species with narrowly defined limits of tolerance would encourage the appearance of endemic species. Theories on the origin and migrations of the temperate mountain vegetation were discussed. These theories are liable to error owing to the absence of evidence from tertiary and quaternary plant fossils and comparative ignorance of the limits of tolerance of South African plants.

ON THE WHEREABOUTS OF THE 'OXFORD COPY' OF RUDBECK'S CAMPI ELYSII

By RUTH GUINEY.

(Communicated by Professor T. G. B. OSBORN, F.L.S.)

It is generally stated by bibliographical authorities that one of the only two perfect copies of Rudbeck's *Campi Elysii* is in the library of the University Department of Botany at Oxford. This is not so. The object of this note is to give a brief account of the book, its wanderings and present whereabouts.

The full titles of this work as given in Krok, *Bibliotheca botanica Suecana*, are as follows :—

Campi Elysii liber secundus, opera OLAI RUDBECKII, Patris and Filii, editus. Then Andre Delen Af Glysis Wald Igenom Olof Rudbäck Fadren och sonen Uthgången och tryckt uti Upsala årh 1701.

Campi Elysii liber primus, opera OLAI RUDBECKII, Patris and Filii, editus Upsalae. Then Första Delen Af Glysis Wald Igenom Olof Rudbäck Fadren och Sonen Uthgången och tryckt uti Upsala årh 1702.

The following short account of Olof Rudbeck the Elder, who first planned this work, is based on that given by Nordenskiöld in his *History of Biology* (1928):

Olof Rudbeck the elder was born at Västerås in 1630, and was the youngest but one of eleven children. He received a thorough education, and was encouraged in natural science studies as a youth. These were greatly aided by his father's possession of a fine botanical garden in the grounds of the College he founded. Rudbeck took up the study of medicine immediately after his entrance to the University, and having matriculated at the age of 17, was moved at once to begin work on his own account, which the poorly equipped Faculty of Medicine rendered it absolutely necessary to do. The observations he made on the chyle system created such a sensation that Queen Christina herself desired to become acquainted with them.

After three years' study in Leyden, he was appointed Professor of Anatomy at Upsala University, carried out many reforms, and built, after his own design, a splendid anatomical theatre which still exists. He found bitter opposition to his practice of dissecting human bodies, but did not allow himself to be deterred. He is said to have been far in advance of Harvey, in denying the property of the liver as a blood-forming organ.

A struggle for priority, carried out with the aid of pamphlets and breaking out in mutual recriminations, arose between Rudbeck and Bartholin for the honour of having discovered the lymphatic duct system in its entirety. It was finally settled that they had come to the same conclusion independently of one another.

Rudbeck is said to have had a tendency to many-sided activities, one being that extraordinary, colossal, linguistic-archaeological patriotic work *Atlantida*, in which he seeks to prove that Sweden is the oldest civilized country in the world.

His childhood's interest in Botany bore fruit, for he devoted much of his life to the production of a large work composed of botanical engravings entitled *Campi Elysii*, but this was never completed.

The anatomical work of Rudbeck's youth chiefly justifies his being regarded as the earliest in the long line of eminent naturalists that Sweden has produced. He died at Upsala in 1702.

The French botanist Amoreux (1825) tells us that Linnaeus seems to have been the first to honour Rudbeck's memory in praising his fine plates, and to have been meticulous in collecting all possible Rudbeckiana. It was Linnaeus who named the genus *Rudbeckia* after him, because the noble family of Rudbeck bore in its arms a kind of Corona solis.

Amoreux further relates that Rudbeck was made Professor of Botany at the University of Upsala, and Director of the Botanical Garden (of which he published three catalogues), and that he was interested in painting and music. He states that Rudbeck was succeeded in the Chair of Botany by his son Olof, who also had a distinguished career.

Of the book itself, Wikström (1831) says (to paraphrase his Latin):

'Olof Rudbeck the elder decided to publish woodcut plates of all the plants known to him, together with their synonyms, intending that his book should supersede all others of the kind. So, partly from other books, partly from his own eyes' witness, he drew some 11,000 plants, coloured the drawings and distributed them among 12 volumes, and then set about cutting the wood blocks. He spent most of his life on this work, and when he grew old, his son Olof diligently carried it on.

'At last, in 1701, the two Rudbecks published the second volume. The reason for publishing Vol. 2 before Vol. 1 was because the drawings of bulbous plants and the like were more in demand than the rest of the Rudbeck figures. Vol. 2 contains about 700 figures of plants of the Liliaceae, Coronarieae, Ensataceae, Orchidaceae, and Orobanchaceae, and in the same pages where the drawings are, the text is printed, giving diagnostic descriptions. In the arrangement they generally followed Caspar Bauhin's *Pinax* (1623). They do not clearly distinguish species from varieties. The figures bring out the habit of the plants fairly well, though in our days they are of little value.

'In 1702, Vol. 1 appeared; it has drawings of the Cyperaceae, Gramineae and Juncaceae.

'The whole of Vol. 2, and all but two copies of Vol. 1 (these being still at the printers) were stored in the cellars of Upsala Cathedral. Here a fire which broke out on 16 May 1702 destroyed most of Vol. 2, and the whole of Vol. 1: the two copies at the printers being all that remained of this volume. Most of the wood blocks on which the drawings were cut also perished*.

'The first quarterly issue of the *Acta Litteraria Sueciae* of 1720 stated that of these two remaining copies, one was in the library of O. Rudbeck the son, and the other in that of Dr. Benzelius the younger.

* The elder Rudbeck is said never to have rallied from the shock, but died in the following December.

' Another writer of about the same date said that only a single copy of this book existed which was in the library of Benzeliuſ.

' And ſtill another informs uſ that the Royal Maſhal and Commander of the King's Order of Waſa, the free Baron Karl de Geer (died 1778) acquired a copy of this rare book, together with ſome of the rare manuſcript volumes, and theſe he kept in hiſ library at hiſ eſtate Leuſta, near Upſala.

' Finally, in a University diſſertation, in 1792, Andreas Lidbeck, Profeſſor of Claſſics at Lund, remarkſ : " Of Vol. 1 only two copieſ ſurvive ; one iſ kept in the library of the University of Oxford, with ſome plateſ miſſing. More copieſ of Vol. 2 exiſt ; the reſt have periſhed."

' From all thiſ it ſeemſ likely that the two copieſ of Vol. 1 from the libraryeſ of Rudbeck and Benzeliuſ came thence into the libraryeſ of de Geer and the University of Oxford ; for of thiſ volume never have more than two copieſ been mentioned with any degree of certainty. Rumour, indeed, had it that three copieſ were extant, but thiſ ſtatement haſ not yet been proved.

' The copy of Vol. 1 which Oxford haſ iſ in the Sherardian Library, in the Botanic Garden. Thiſ copy lackſ the title-page, and compriſeſ pp. 1-224, whereof pp. 41-48 are miſſing, but were afterwards reſtored in pen and ink. I do not know, when or how thiſ copy reached Oxford.' (End of the Latin paraphraſe).

The copy of thiſ beautiful work formerly in the poſſeſſion of the Sherardian Library at Oxford waſ, in fact, reſtored to the Swediſh authorityeſ in 1862, and iſ now in the Kungliga Bibliotek at Stockholm. The reference to iſ exiſtence in Oxford occurſ in Pritzel (1872), Jackson (1881), and the Proceedingſ of thiſ Society, 1887-88 (it iſ here that we are told that the de Geer copy had been loſt ſight of, making our copy unique). However, the de Geer copy muſt have ſince come to light, aſ Mr. Colliander, deputy librarian at the University of Upſala informſ uſ in a recent letter, that ' it iſ very exactly deſcribed ' in *Bibliotheca Rudbeckiana* by J. Rudbeck, Stockholm, 1918. A further reference to the de Geer copy waſ received a few dayſ ago from Mr. Wieſelgren, chief librarian to the Royal Library, Stockholm (where the copy formerly in our poſſeſſion now iſ). To quote : ' . . . the other exiſting copy belongſ to the collectionſ of the Swediſh family de Geer at the Caſtle Lõſta (Province of Uppland). Thiſ copy iſ complete and haſ the pageſ miſſing in the copy in the Royal Library.'

From theſe two letterſ we alſo gather that ſmall fragmentſ of Vol. 1 are to be found in the University Library of Upſala, the library of the late Baron J. Rudbeck at Stockholm, the library of the Britiſh Muſeum, and that poſſibly ſome leaveſ may alſo have come to the Public Library of Leningrad with the collectionſ of the great collector Count Suchtelen, who iſ ſaid to have bought them when he waſ Ruſſian miniſter at the Swediſh court. The third copy of the book ſpokeſ of in a Swediſh catalogue in 1757 probably never exiſted.

My attention waſ firſt drawn to the reputed exiſtence of the book in Oxford when reading Ellacombe's *In my vicarage garden* (1902). On conſulting the catalogue it waſ diſcovered that the book waſ no longer there. Dr. G. C. Druce alſo knew that thiſ waſ ſo, but I am not aware of any record having been made by him, other than a marginal manuſcript note in our copy of Jackson's ' Sketch of the life of William Sherard ', *Journal of Botany*, 1874. Thiſ correctſ Jackson's reference to Sherard's poſſeſſion of ' a ſuperb copy of the *Campi Elyſii*, the firſt book, without colophon, but probably the moſt complete copy extant.' Jackson alſo informſ uſ that through ſome miſapprehenſion Sir J. E. Smith believed that a copy of the rare Vol. I would be included with the Linnaean treaſureſ ſent to him from Sweden in 1784, but thiſ proved not to be ſo. The treaſureſ did include, however, ſome of the wood blockſ of Vol. 1, and proof-impreſſionſ of theſe were printed by Smith in 1789.

In 1722 the Rudbeck *Campi Elysii* from Benzelius' library was indeed sent to William Sherard, who endowed the Chair of Botany at Oxford, to be used in connexion with his own 'Magnum Opus', the Sherardian Pinax. It is relevant here to quote what Jackson tells us of this work.

'Whilst staying in this city (Rome) he (Sherard) seems first to have seriously contemplated what afterward became the dominant object of his life, namely the continuation of Caspar Bauhin's Pinax (1623), by the incorporation of all subsequent synonymy and discoveries, Tournefort being the instigator of the work.'

Sherard at first believed the Rudbeck to be a gift, since Benzelius' letter, which would have made the matter clear, never reached him, and Sherard writes :

à LONDRES le 15 octobre 1723

Au tres Reverend Le Rev'd
Monsieur Eric Benzelius a Upsala]

Je suis fort fâché que la lettre que vous m'avez fait l'honneur de m'écrire soit perdue . . .

Le jour que je devois m'embarquer pour l'Hollande, notre ami commun Mr. dela Motraye me portait de votre part, Monsieur, les *Campi Elysii* de Messrs. Rudbeck, livre si rare, que sans votre genereuse communication je n'aurois pu l'enregistrer dans le Pinax de Bauhine . . .

Permettez moy donc Monsieur de vous en rendre mille grâces et de vous supplier de me faire sçavoir ce qu'il y a pour votre service dans ce pais-cy. Je sçai bien que vous-etes curieux en livres, et vous ne pourrez m'obliger plus qu'en m'envoyant une note de ceux que vous souhaitez; s'il y a quelque autre choses pour votre service, donnez-moy les occasions de vous temoigner avec combien de sincerite et de passion je suis, Monsieur,

Votre tres humble et tres obeissant serviteur,

GUILL^e SHERARD.

Nearly two years later we find Sherard writing to a correspondent whose name is missing :

Towerhill, LONDON.

July 27. 1725

Dear S^r.

Since you were pleas'd to advise me of y^e receipt of my letter to Dr. Bentzelius, & of the arival of the Box of Books sent to him & other friends at Upsal . . .

Knowing y^e rarity of y^e first volume, I desir'd Mons^r. dela Motraye, to write to his freind, y^t I might have y^e perusal of it, (being necessary to a work I was upon) & y^t if he cou'd procure it me, I wou'd insure it hither & back again, at whatever value shou'd be set upon it. it was brought over by Baron Sparr & deliver'd to me by Mr. dela Motraye who read to me part of a letter from Dr. Benzelius, wherein he mention'd y^e scarcity of Rudbeck, but y^t being acquainted wth my design of reprinting C. Bauhine's Pinax, & how necessary it wou'd [be] to me, he thought it better plac'd in my library than his own . . .

I wish S^r. you cou'd set me to rights in this affair. I have defer'd writing sooner, in hopes of Mr. Dela Motrayes return from Holland, y^t I might have seen y^e letter he read to me, and desir'd he wou'd have informed himself of y^e occasion of these mistakes, but I don't hear when he designs to come back.

if he has led me into an errour (as may be suppos'd from what was wrote to Dr. Jurin) I am very ready to return Dr. Rudbecks book, & shall think myself well satisfied by y^e perusal of it for what I sent . . .

Dear Sr.

Your obliged humble serv^t

W. SHERARD.

It will be seen from these letters that Sherard could not succeed in obtaining a confirmation of his understanding that the book was a gift. He died not long after, in 1728.

Nothing further was heard of the book until 1862, about 140 years later, when the Swedish Ambassador in London, Count Wachmeister, visited Professor Daubeny, who then held the Sherardian Chair of Botany in Oxford. By this time the Swedish authorities had come to the conclusion that the book was a loan, not a gift, and that Sherard's letters (from which the above excerpts are taken) could be interpreted to indicate this. The Ambassador gave Professor Daubeny facsimile copies of the letters; these are in the Manuscript Collection of our library.

Wachmeister writes to Professor Daubeny upon his return to London :

SWEDISH AND NORWEGIAN LEGATION,

Private.

LONDON,

December 12th 1862.

Dear Sir :

With reference to the conversation I had with you yesterday at Oxford, I avail myself of your kind offer to employ your good offices with the University of Oxford in behalf of the Swedish Government's desire to be able to recover a precious book, the first volume of Olof Rudbeck's *Campi Elysii*, being the only copy of this volume now existing, and consequently of very great value to the Royal Library of Stockholm . . . from some misunderstanding, owing to a lost letter, it [the book] was never returned to Upsala. From the copies of several letters from Sherard which I had the honour of placing into your hands yesterday, you will, I presume, recognize the exactitude of this statement, and also that Sherard himself seems to have had the intention to send back the book.

A decision to return the book to Sweden must have been made almost immediately after by the University Authorities, as the following entry appears in Daubeny's diary only a fortnight later :

26 December 1862

'I have this day forwarded to his (the Swedish Ambassador in London) address the volume of Rudbeck's *Campi Elysii* which had been so long in our possession.'

And :

27 May 1863

'Reported to the Vice-Chancellor what had been done with respect to the restoration of the copy of Rudbeck's *Campi Elysii*.'

In return a photographic copy of Vol. 1 and an original of Vol. 2, finely bound as one volume, were sent to Oxford.

The facsimile volume is of additional interest as one of the earliest examples of photographic reproduction of an illustrated book.

Grateful acknowledgement is due to Mr. E. Colliander, deputy librarian, University of Upsala, and to Mr. O. Wieselgren, chief librarian, Royal Library, Stockholm, for references and information used in the preparation of this note, to Mr. R. Burn for his translation of the Wikström, and to Professor Osborn for his interest.

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Exhibits.

From the Department of Botany, The University, Oxford :—

- (a) The volume containing the facsimile of *Campi Elysii liber primus*, and an original copy of *liber secundus*.
- (b) The MS. diary of Professor C. G. B. Daubeny, containing the facsimiles of William Sherard's letters and the correspondence with the Swedish Ambassador.
- (c) A folder containing a portion of the Sherardian Pinax, in the handwritings of William Sherard and J. J. Dillenius.

From the library of the Linnean Society :—

- (d) 23 leaves of proof-impressions of some of the woodblocks used in *Campi Elysii liber primus*. There is no printed text. (Linnaean Collections.)
- (e) *Campi Elysii liber secundus* from Linnaeus's library. Its collation agrees with that of the Oxford copy.
- (f) *Reliquiae Rudbeckianae* . . . cura J. E. Smith, Londini, 1789.
- (g) Some of the original woodblocks for *Campi Elysii*. (Linnaean Collections.)

Discussion.—

Mr. S. SAVAGE called attention to the collection of proof-impressions of some of the woodblocks used in the first volume of *Campi Elysii*; and to the statement by Krok, *Bibliotheca Botanica Suecana*, 1925, p. 605, that the facsimile of the first volume, made in 1863, was limited to 20 copies and issued by P. H. Mandel, Stockholm. He also suggested that the intimate connection between the plants figured in *Campi Elysii* with the specimens in Burser's Herbarium was the reason why Linnaeus so seldom cited Rudbeck's work.

Mr. W. T. STEARN congratulated the speaker on the success of her investigation which had certainly shattered the widely held belief, based on Pritzel's *Thesaurus*, that the Oxford Botanic Garden possessed the only copy of the first

volume of the *Campi Elysii*. He called attention to the uneven quality of Rudbeck plates which had been copied for the most part from earlier works and were some of them so inaccurate that Linnaeus could well be excused for not citing them.

Professor T. G. B. OSBORN drew attention to the interest of such a large-scale use of photolithography as early as 1863.

EDMUND DAVALL'S NOTE BOOK

By G. R. DE BEER, F.R.S., Pres.L.S.

[Read 10 March 1949].

Scarcely had I passed the proofs of what I thought was going to be the final addendum to my paper on Edmund Davall, when I received from his great-grand-daughter, Madame M. Hager-Davall, the note book which he used to record some of his seasonal observations. It is a copy of *The Naturalist's Journal* (London, 1775), drawn up by Daines Barrington, the book used by Gilbert White for his *Journal* and described by Walter Johnson. Probably in emulation of Benjamin Stillingfleet's *Calendar of Flora*, Davall has added to the title of his note book the words:—'At Orbe in the Canton of Bern in Switzerland. Latitude 46°, 49'.' He also followed Stillingfleet in the adoption of the abbreviations used to specify the seasonal condition of the plants referred to, as follows:—

B, buds beginning to open; **E**, emerging out of the ground; **F**, flowers full blown; **f**, flowers beginning to open; **L**, leaves quite out.

It will be noticed that Davall was also attentive to the fauna of his neighbourhood.

From the point of view of his biography the chief information supplied by this note book is that he was at Orbe in 1783 before his father's death. The last entries in his note book coincided with the start of his voluminous correspondence with Sir James Edward Smith and with the onset of his disease.

No especial value is attributed to this note book, but it possesses the interest which any good record of field observations must always command, particularly in an out-of-the-way station in the 18th century, and provides a picturesque record of the activities of one of the first Fellows of the Society.

In the following records, observations of temperature, wind and weather, where made, come immediately after the date. The strength of the wind is recorded on Daines Barrington's scale by which the figure 4 denotes 'a storm, in its greatest violence'. The temperature is recorded on Reaumur's scale.

1783

August 16th Phalaena N. Gamma.

1784

Jan:^{ry} 31st The Strix Aluco given me.

Feb:^{ry} 2nd NNE. Snow. Several flights of wild geese. Anas Anser or ferus.

3rd A great number of wild geese settled on our corn-lands.

13th NNE. Snow. Wild geese still appear. A Bustard shot about 5 miles from hence, one was also shot near Lausanne 10 days ago. Otis Tarda not Tetrax.

1784

Feb:^{ry} 26th

SWS. Thaw. The Chaffinch, *Fringilla caelebs*, has sung for some days past. *Aestatis Nuncius* !

In Feb:^{ry} in the woods near Sergey, I saw a considerable number of small birds on the birch-trees which seemed to delight in fixing themselves to the pendulous branches, hanging by their feet, & in that position pecking the catkins : I shot one, which I have since found to be *Fringilla Spinus*.

March 12th

Scarabaeus fimetarius.

22^d

Snow. *Upupa Epops* given me. The *Upupa Hoopee* took shelter in a tower on account of the sudden return of cold.

29th

Daphne Mezereum. **F.** *Meloe Proscarabaeus*.

April 14th

Snow. *Anemone Pulsatilla* : as also the *A. Hepatica* : **F.** & sooner. Mr. Roland gave me the *Fulica atra*.

23^d

Narcissus Pseudo-Narc : **F.** Heard the first Cuckow.

August 13th

Paris quadrifolia fruit ripe. Pap. Apollo seen.

N.B. The interruption occasioned by my journey to England.

Nov:^r 17th

Mr. Roland gave me a cock & hen of the *Tetrao Bonasia* shot in y^e mountains of la Vallée du Lac de Joux.

Dec:^r 15th

Snow on the ground.

1785

Feb:^{ry} 28th

N.2. Snow on the ground. Steel Nights. Wainscot cracks. *Strix Aluco*—obs. Irides deep brown : pupils bluish—*Remiges*.

March 2^d

1st 2 inches shorter than 2^d.—2nd 1 inch shorter than 3^d : 4th & 5th longest :—Bill at the point somewhat transparent : yellow—the rest greenish.—extent of wings 3 ft. 1 inch. 1st & 2nd quill-feathers serrated.—Tail the longest of the *Rectrices* 5 inches measured from the end of the *Uropygium*. Tail 6 inches or more.—Face grey : encircled by a line of neat scolopacine plumes.—Predominant colour on the upper parts brown—Leg-feathers white, mottled with light-brown.—

11th

Var. between W & N. Snow on the ground. Gentle thaw.

12th—13th

8 a.m. 2° below 0. point of congel. NE by N. 3½. Frost. In the night a considerable fall of snow added to what has lain on the ground wth little diminution since the beginning of Feb:^{ry} and still earlier ?

14th

12 noon. 1° below 0°. 4 p.m. 2° d°. 9.30 p.m. 4° d°, NE. 3½ frost. As the snow came by a high wind it is very deeply collected in many places, so that the inhabitants are obliged to work at clearing the roads, carting from the streets & c or furnish a certain sum (2 batzes=3 pence, English) towards pay of hired workmen.—not remembered by persons above 80 at this season.

15th

8 a.m. 2½° below. 12 noon. 1½° d°. 4 p.m. 1° d°. 9.30 p.m. 3° d°. NE by N. 2. Frost in the shade. In the sunshine the eaves drop.

20th

Sunday. Vernal Equinox. 12 noon 6½°. NNW. & N. by W. Thaw. Chaffinch, *Fringilla Coelebs* sings but little. *Aestatis Peroptata Praedicatrix* !

Mem : 19 recruits for a Swiss Regiment in the King of Sardinia's Service were destroyed by an avalanche this winter in passing the Grand St Bernard.—

24th

8 a.m. 2° below. 4 p.m. 1° below. NNE. 2. Frost.

N.B. A man aged 96 who died last week at Baume did not remember to have ever seen such severe weather at so advanced a season.

1785

March 25 th -26 th	8 a.m. 1° below. NW by W. 12 noon at 0. N by E.
27 th	8 a.m. at 0. WNW. 12 noon 4½°. SSW. Easter-Sunday..
28 th	8 a.m. 1°. S by W. 2. 12 noon 1½°. 4 p.m. 1½°. W. 9.30 p.m. 4° below. Sleetish snow. Chaffinch Fringilla, coelebs sings.
29 th	8 a.m. 3° below NW. by W. 12 noon at 0. N by E.. 4 p.m. 2° below. 9.30 p.m. 3½° below. Hard frost last night. Small snow.
30 th	8 a.m. 1° below. NNW. 12 noon 3° N by W. 4 p.m. 3° NW. 9.30 p.m. 5° below. 9 or 10 inches of snow.
31 st	8 a.m. 3½° below. N by W. 12 noon ½° below. N. 4 p.m.. ½° below. 9.30 p.m. 6° below. Very hard frost last night.. Fringilla montifringilla found dead in one of our windows.
April 1 st	8 a.m. 3½° below. WNW. 12 noon 1½° N by W. 4 p.m.. at 0°. Snow. 9.30 p.m. 2° below. Very hard frost, last night.
2 ^d	8 a.m. ½° NW. Foggy 12 noon 5° W. 5 p.m. 2½° S.. Sleet 9.15 p.m. at 0.
3 ^d	8 a.m. ½° below. NE by N. 12.30 p.m. 3° 4 p.m. 1° NNE.. 8 p.m. 2° below. Very considerable addition of snow during the night.
4 th	8 a.m. 1½° below N by E. 12 noon 1° NE by N. 2½.. 8 p.m. 2½° below.
7 th	8 a.m. 2° below NE. 12 noon 1° NE. by N. 4 p.m. 1° N.
8 th	8 a.m. 2° NNW. 12 noon 6° 4 p.m. 4° N by W. 8 p.m. 2°.
9 th	8 a.m. 4° N by W. 12 noon 7° NE by W. 4 p.m. 4° 8 p.m. 2° New Moon. Thaw. Ardea Grus. The descriptions of Linnaeus, Scopoli & Pennant ; excellent.
10 th	8 a.m. 5° NE by N. 12 noon 4° 8 p.m. 2° Thaw.
11 th	8 a.m. 6° NNW. 12 noon 6° NNE. 4 p.m. 5½° 9.30 p.m. 3° Thaw. Leucoium vernum. F. Pollen Ovale, subreniforme. Crocus Sativus, F.
12 th	8 a.m. 6° N. 9.15 p.m. 2°. Thaw. Hirundo rustica. appears. Papilio Rhamni appears & 2 or 3 others.
13 th	8 a.m. 3½° WNW. 12.30 p.m. 7° SE by S. 9.15 p.m.. 2½° Thaw. Ribes nigrum. B.
14 th	8 a.m. 7° WNW. 9.40 p.m. 3° Thaw.
15 th	8 a.m. 7° N by E. 11.45 a.m. 6½° NE. 8 p.m. 4½° Thaw.. 16 th
16 th	8 a.m. 6½° NNW. 9.30 p.m. 4½° Thaw. Primula veris.. acaulis. F.
17 th	9.30 p.m. 6½° Thaw. Arum maculatum. L. Tussilago- Farfara. F. Veronica hederaefolia. F. Both at Grandson.
18 th	9.30 p.m. 7½° Gentle rain. Corylus Avellana. F. & perhaps earlier. Papilio Antiopa. Scarabaeus Stercorarius. S. Fimetarius.
19 th	8 a.m. 7½° WSW. Misty. 12 noon 12½° S by W. 9.30 p.m. 8°. The ground has been covered w th snow with hardly any interruption from the 17 th Dec'r, a considerable quantity still remains by hedge sides, &c &c & in the higher ground nearer the Mountains.
20 th	8 a.m. 8° SW. Rain. 10 p.m. 6° Anemone Hepatica F. & also Helleborus foetid. Heard & saw the first cuckow.

1785

April 23^d

8 a.m. 5° WNW. 12 noon 9° NE by E. *Ardea Nycticorax rara*!! avis. Feet more yellow than the Lora.—*Caput et dorsum atro-viridans*. Iris, *coccinea*, *pupilla nigra*. Kramer.

27th

9.30 p.m. 3° NE. 3. *Arum mac.* *Spatha* out. *Ranunculus Ficaria*. F. Both on the Road to Yverdun.

28th

8.30 a.m. 4° NE by E. 3½. 10 p.m. 2°.

29th

9.30 p.m. 3° NE by E. 3½. *Vinca minor*. An: *nemorosa*. *Pulmonaria* off; F. I offer'd an handful of the An. *nemorosa* wth 2 plants of the *Pulmonaria* offic: to a goat: 1 the 1st—0 the 2.

30th

9.30 p.m. 5° N by E. *Caltha palus* & *Fumaria bulbosa*. F. Nightingale? or very probably the *Motacilla atricapilla* sings. Some snow still remains on the roadsides—the the ground however at last re-appears on the Jura. Such continued snow and a winter so drearily sustained are not remembered. The usual spring employment of the husbandman has been so much retarded that the customary reviews of the Militia have been omitted. The peasant handles his plow and neglects his musket. O fortunatos nimium sua si bona norint!

May 1st

4 p.m. SSW. 9.30 p.m. 5° *Hyacinthus racemosus* & *Euphorb.* Cyp. F.

2^d

8 a.m. 8° S by E. 12 noon 8½° NE by N.

3^d

Anemone Pulsatilla & *Tussilago Petasites*. *Fumaria bulbosa* var: flore albo.

4th

Ranunculus auricomus. f: *Apis* *Violacea* about the Peach blossom.

5th

9.30 p.m. 10°. *Cardamine pratensis*. F. *Chrysomela Populi*. in *Salice*.

6th

Anemone ranunculoides. F.

7th

Orobis vernus has been in flower for some days past.

12th

On Suchet. F. *Crocus vernus* *Wulfenii* & *Draba aizoides*.

14th

Tetrao Urogallus mas. Tail feather 18, *Scopoli's* description excellent, in his crop small branches of *Vaccinium Myrtillus* & *Pinus Picea* chiefly. some berries of *Berberis* ? ? & *Vaccinium Oxycoccus*?

16th

Mespilus Amelanchier. *Globularia vulgaris*. F. *Euphorbia pilosa*?

17th

Lon. Xylost. *Genista* Germ. *Teucrium Chamaepity.* *Orchis purpurea*.

19th

Paris quadrif. *Melittis*. *Melissophyl.* Conv. *maialis.* *Anthyllis Vulneraria*.

22^d

Veronica Chamaedrys. *Orchis Morio.* *Geranium molle.*

28th

Geranium sanguineum. *Asperula odorata.* *Orchis latifolia.*—*Mascula.*

30th

9.30 p.m. 8° *Crataegus Oxyacantha* has begun flowering these few days past. *Coronilla Emerus* has been in flower some days past.

31st

8 a.m. 9°. Snow on the Mountains. Suchet &c &c *Nymphaea lutea* & *Ranunculus aquatilis.* *Thalictrum aquilegifolium.*

June 1st

8 a.m., 9°. More snow on the Mountains. *Evonymus europaeus.* *Ophrys ovata.* *Saponaria Ocyroides.*

1785

June 5th *Pinguicula vulgaris*. *Primula farinosa*! *Narcissus poeticus*.
Trollius europaeus. *Pedicularis palustris*. The snow not
all melted on the highest of the Jura.

6th *Lotus siliculosus*. **F.** Cows go to the Mountains.

8th *Atropa Belladonna*. **f.** *Echium vulgare*. *Scrophularia*
nodosa. *Potentilla Anserina*. *Reseda lutea*. cum multis
aliis. *Myrmeleon Libelluloides*!!! *Scarabaeus lunaris*.

14th *Ophrys Muscifera*. *Geranium Sylvaticum*. *Reseda luteola*.
Althaea hirsuta! but much less than in Jacquin's figure.
Fl. Austr. Tab: 170.

25th While I stopt in a wood to gather *Pyrola rotundifolia* et
secunda. **f.** I observed that my horse eat of the *Aquilegia*
vulgaris. He refused 2 species of *Melampyrum*.

July 1st *Valeriana officinalis*. **F.** *Papilio Apollo* first seen.

5th *Gratiola officinalis* and *Oenothera biennis*. **F.**

6th *Lythrum Salicaria* **F.**

10th On Suchet. *Saxifraga Aizoon* Jacquin & Sax: *rotundifolia*,
Thymus alpinus. **f.** *Aconitum Napellus*. **F.** *Digitalis*
ochroleuca. **F.** *Valeriana* & *Centaurea montana*. *Aconitum*
Lycotconum. **F.** *Osmunda lunaria*.

15th *Monotropa Hypopithys*. **F.** *Ursus Meles* killed yesterday
evening in a wood by the Goat herds—a female out before
night probably to search for food for her young.

19th *Prenanthes purpurea*. **F.** *Meloe Vesicatorius* in *Ligustro*.
Anthericum ramosum. *Linum tenuifolium*.

August 31st *Colchicum autumnale* and *Scabiosa Succisa*. **F.**

Sept:^r 2^d My horse eat of the *Lycopus Europaeus*.

11th *Gentiana Pneumonanthe*!

Oct:^r 10th Cows come down from the Mountains.

27th Snow on the Mountains.

Nov:^r 30th Wind & rain for some days past, Rivers & ditches overflowed.

Dec:^r 23^d *Potentilla verna*—*Geranium robertianum*. *Polygala vul-*
garis.—**F.** along the rill beyond the grotto of Montcherand—
a situation exposed to S. & sheltered by rocks. First Snow.
A light fall of snow in the night.

24th Small gentle snow.

25th X^tmas Sunday. 8 a.m. Small gentle snow. It continued to Snow
gently all the last day & night; so that it is already more
than a foot deep.

1786

Jan:^{ry} 7th 8 a.m. S. by W. Rain. The cold N.E wind which has reigned
for several days past w:th hard frost is come about to the
S by W w:th rain.

8th An inundation of Snow Water.

14th Fine. *Leucoium vernum* **E.** *Lamium purpureum* *Thlaspi*
B[ursa].P[astoris]. **F.** Since the 8th the weather has been
uncommonly mild for the season. Very little frost—some
fine days, others rainy—so much rain during the 15 that
there is a new inundation.

19th 8 a.m. NNE. Snow. From the 16th the same damp rainy
weather: on the 18th in the evening the wind came about
to the NNE w:th snow in the night.

28th & 29th S. by SW. Fine weather snow melts very fast hardly any
left in the evening of 29th.

1786

- Jan:ry 31st Wind come about to N: & NE: w:th frost.
 Febry: 1st D^o.
 4th Ardea cinerea killed.
 5th & 6th? N.W.
 8th & 9th Rainy.
 17th S by W. Primula acaulis. **F.** Papilio Rhamni. The weather very fine for 2 or 3 days past.
 18th Arum maculatum. **L.** on the road to Yverdun. Daphne Mezereum. **f.** Papilio Urticae. Fine weather continued. Corylus Avellana. **F.**
 21st N by E. NE. Wind come about to N & NE with frost.
 22th 23^d 24th Cold continues.
 24th, 25th Snow.
 25th, 26th D^o
 March 2^d 4 p.m. S. Somewhat rainy. Snow nearly all melted.
 5th N — ?
 6th N by E. Snow wth cold wind.
 7th Thaw.
 8th Frost. 8 a.m. WNW.
 9th NE by N. Frost.
 10th NNE. d^o
 11th d^o d^o
 12th S. Thaw.
 13th d^o d^o 4-8 p.m. rain. Motacilla alba?
 14th ? d^o Rainy.
 15th 8 a.m. NW by N. Rainy.
 16th Hazy. Leucium vernum. **F.**
 17th Rainy. Crocus. **F.**
 20th Vernal Equinox. Anemone Hepatica. **F.**
 23^d Motacilla Phoenicurus.
 25th Draba verna. **F.**
 26th Snow on Mountains in the night.
 27th Sleet & snow.
 28th Snow.
 29th 8 a.m. Snow melts in the Sun. 4 p.m. NNE. In Woodcock shooting in le Bois de Chabagne, a dog took a bird on the nest w:th 4 eggs. The dog eat one *I have one*.
 April 1st Fumaria bulbosa. **F.** Snow nearly all melted.
 9th Rain.
 10th 4 p.m. NE by N. A great inundation.
 11th, 12th, 13th NE. by N. 2 & 3.
 23^d Saxifraga tridactylites. **F.** Heard the first Cuckow.
 26th Orchis Masculata. Fine weather for some days past.
 29th Globularia vulgaris. Fine weather has continued.
 30th Rain.
 30th-1st Rain.
 May 1st Rain. The river begins to overflow. Much water in the Marshes.
 June 7th on Suchet. Bartsia alpina. **F.** & **f.** Crataegus Chamaepspilus. **f.** Anemone alpina & narcissiflora. **F.** Gentiana verna & acaulis. **F.** Ranunculus aconitifolius. **F.** The proper time for visiting the Jura & still earlier. Saxifraga Aizoon. **f.** &c. &c., &c., &c.
 Since my return from my journey in the Alps & the Baths of Leuck I have too much neglected this journal—the Autumn steals on us apace. The Colchicum autumn has flowered at least a fortnight earlier than last year.

1786

Sept.: 24th, 25th Snow on the Jura. Roche Blanche, &c &c.

October Cold weather has continued from snow on Mountains—NE. wind has lasted nearly till now.

30th

First Snow. The Poor People are obliged to vintage in the snow as it was little more than half finished.

Nov.: 3^d

Strix Ulula. My bird without any doubt the *Noctua flammatra*. Length 15 inches measured from the occiput to the end of the tail when laid on the belly.—and extent of wings 3 feet 2 inches & extended as much as possible. Length 12 inches—as I know not the usual method of measuring—I laid my bird on his back in an easy posture when dead & measured without any extension from the point of the bill to the end of the claws. Iris of a most beautiful bright yellow: very narrow: this may betray my ignorance I know not whether or no the pupil is capable of dilatation & restriction in animals which have the nictitating membrane. I had my bird alive & did not perceive any alteration in the eyes on holding him to a window, perhaps his agony from his wounds might have some effect. How that is I know not, seeing him suffer I immediately put an end to his misery. The pupils black. Bill black. Immediately about the eyes black, especially on the off sides. Face white only under the bill, in the space between the bill & the eyes & half way over the eyes so that the white forms an horse-shoe. The head if my memory does not mislead me less in proportion than in the *Aluco*, face less flattened. 1st and 2^d quill feather serrated the 2^d only for the length of 2½ inches from the end 1st in its whole length. 1st quill feather about an inch shorter than 2^d—2^d longest of all—the general colour & disposition of the plumage elsewhere much as in Pl. Enl. 438 which cannot be called bad altho' it does not exactly render my individual—the fundamental colour in mine lighter & more on the buff—the spots on the upper parts near the back less distinct. Tail feathers 12. Barred with the Brown & rufous which predominate all over the bird. In the 2 central tail feathers the pale colour does not form the bar not arriving either at the shaft or edges of the feathers therefore appears in 2 rows of spots and moreover these pale spots inclose other spots of the fuscous colour & form eyes. There is some slight disposition to this arrangement on one feather on each side these 2 but less notable all the others are *barred*, their extremities pale. Femora & Tarsi spotless of nearly the same pale colour as the ground of the belly in a slight degree less pale & brighter (more silky) feathers down to the claws which are black. Some time after I examined another specimen of *Strix Ulula* perfectly agreeing with the last only the markings of the tail feathers were somewhat less distinct & slightly different perhaps from difference of age.

1787

March 1st

We have had little snow this winter—long continued frost & for some time past thaw in the day w:th frost at night. *Leucoium vernum*. F.

1787		
March	2 ^d	Somewhat rainy. Frog appears.
	3 ^d	Same.
	4 th	Rain last night. River swells.
1788		
April	16 th	Ornithogalum nutans. F. First Cuckow. Polygala amara— Cardamine pratensis—&c, &c, &c. in full flower.
May	9 th	Discovered the Hypnum aquaticum in the Orbe near its re-appearance at V[allorbe].
1792		
July	8 th	Saxifraga Hirculus in the great peat bog near St Croix. Eriophorum alpinum with down expanded. Scheuchzeria palustris fruit at $\frac{1}{2}$ growth therefore to be found in flower about the middle of June or rather later ?

PROCEEDINGS OF THE GENERAL MEETING ON 20 January 1949

Professor G. R. DE BEER, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 6 January 1949, have been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mrs. Vera Higgins, the late Dr. G. H. Pethybridge, Colonel F. C. Stern, O.B.E., M.C., the National Museum of Wales, Cardiff, and the Editor, 'History and Bibliography', Christchurch, N.Z.

The President reported the death of Mr. Iain Macbeth Cooper Talman, Fellow of the Society.

The following communications were read and discussed :—

Mr. N. G. STEPHENSON. Observations on the development of the Amphicoelous Frogs, *Leiopelma* and *Ascaphus*. (With photomicrographic illustrations of development in both genera.) (Discussed by the President, Dr. Malcolm Smith and Dr. S. M. Manton.) [To be printed in full in the *Journal, Zoology*.]

Dr. H. A. BAYLIS. *Fecampia spiralis*, a cocoon-forming Parasite of the Antarctic Isopod *Serolis schythei*. (In the author's absence, Dr. Maurice Burton gave an account of the paper. Discussed by Dr. S. M. Manton and the President.) [Printed in full below.]

Dr. R. N. SALAMAN, F.R.S., and Dr. J. G. HAWKES. The Character of the Early European Potato. (Discussed by Mr. I. H. Burkill, Dr. R. Melville, Mr. A. H. G. Alston, Mr. W. T. Stearn, the President and Mr. S. Savage; Dr. Salaman replied.) [Printed in full, p. 71.]

The following paper was read in title :—

'Some Suggestions on the history of Potato Virus X.' By J. E. VAN DER PLANK, Division of Botany and Plant Pathology, Pretoria. [Printed in full in *Journal, Botany*, No. 352.]

FECAMPIA SPIRALIS, A COCOON-FORMING PARASITE OF THE ANTARCTIC ISOPOD SEROLIS SCHYTHEI

By H. A. BAYLIS, M.A., D.Sc.,

Department of Zoology, British Museum (Natural History).

(Plates 3 & 4, 8 Text-figs. and a sketch map.)

In the summer of 1947 Dr. M. Burton drew the writer's attention to some curious objects (Plates 3, 4) attached to the dorsal surface of the Antarctic Isopod, *Serolis schythei*, in the collections of the 'Discovery' Expedition. These had been noticed by Mr. R. Bassindale, of the University of Bristol, who, thinking that they might be sponges, had consulted Dr. Burton about them. Subsequently, through the kind offices of Dr. H. E. Bargmann, a large number of the Isopods, many of which carried these objects, was made available for study.

Dr. Bargmann also very kindly examined the 'Discovery' material of other species of *Serolis*, seven of which had been taken in association with *S. schythei* on various occasions, but was unable to find the objects on any of them. Further, the writer examined trawl residues from many of the hauls made by the R.R.S. 'William Scoresby' at stations where *S. schythei* was obtained, in order to determine whether the objects occurred on other animals or on stones, shells, seaweeds and the like, but they were never found attached to anything but *S. schythei*. There seemed, therefore, to be a definite association between the objects and this particular crustacean.

The stations at which these objects were obtained (see Chart) are on the Patagonian continental shelf, almost all at depths of less than 200 metres, and mostly to the North of the Falkland Islands. They cover the greater part of the known range of *Serolis schythei*, which occurs on the sea-floor in this area at depths varying between 60 and 300 metres (Sheppard, 1933). The dates shown against the stations on the chart do not all refer to the same year, but cover portions of the years 1927, 1928, 1931 and 1932.

At a fairly early stage of the investigation the nature of these objects suggested that they might be 'cocoons' secreted by some worm-like animal, and further study has afforded support to this idea. The objects will, therefore, henceforth be referred to as cocoons. It was at first thought likely that the animal that produced them would prove to be a Nemertine, but when the animal was discovered it seemed difficult to reconcile its characters with those of that group. The writer is indebted to Dr. Carl Pantin, F.R.S., for making the very useful suggestion that it might be related to *Fecampia* Giard, 1886, an aberrant genus of Rhabdocoele Turbellaria. There seems to be very little doubt that it does, in fact, belong to that genus, or at least is very closely related to it.

THE COCOON.

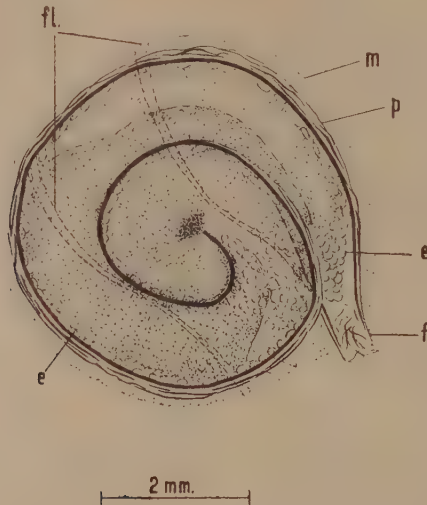
The cocoons are very easily detached from the *Serolis*, a slight push with a needle being sufficient to dislodge them from preserved specimens. When they have been thus removed, nothing remains on the integument of the *Serolis* to show where they were attached.

On examination, each cocoon (Text-fig. 1) is found to be a parchment-like tube coiled into a close, flat spiral, varying from about 3 to 7 mm. in diameter, with one end free, tapering and apparently having a terminal opening guarded by a membranous frill. The upper surface is somewhat convex, and the lower surface more flattened and moulded exactly to the shape of the surface of the *Serolis*, usually with projecting flanges fitting into the interstices between the



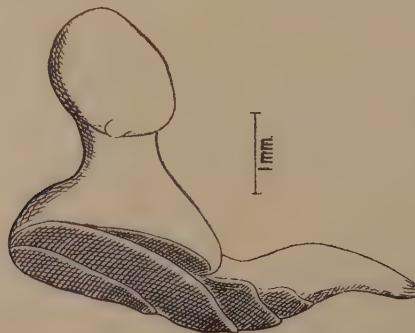
Chart of the Patagonian Continental Shelf, showing the stations at which *Serolis schyskei* with cocoons were obtained, with dates.

dorsal plates. Two layers are recognizable in the walls of the cocoon, there being a more delicate and transparent outer layer, evidently composed of mucus, and a relatively tough inner layer which is much more opaque and parchment-like, and is drawn out at the free end into a kind of frill round the opening. This frill would probably make it difficult for anything to enter, but would allow small larvae to creep out.



TEXT-FIG. 1.—A cocoon detached and viewed from above as a transparent object. *e*, eggs; *f*, free end of cocoon, with membranous frill; *fl*, flanges on lower surface between plates of *Serolis*; *m*, outer mucous coat of cocoon; *p*, inner parchment-like coat.

There may be only one cocoon, or sometimes two or three, on a single *Serolis*. With few exceptions, the cocoons are situated towards the sides of the hinder thoracic segments. One was found completely covering the left eye of



TEXT-FIG. 2.—A cocoon of unusual shape, detached and viewed from the side.

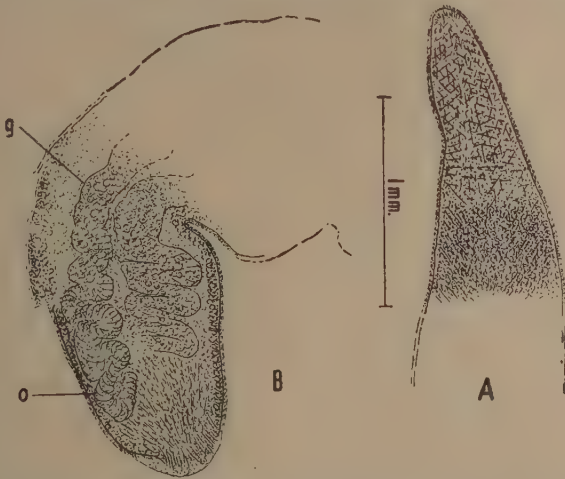
a *Serolis*. A curious point is that the direction of the spiral of the cocoon generally seems to be determined by its position. If on the left side it is almost invariably sinistral; if on the right, dextral. In either case the free end almost always projects laterally and somewhat posteriorly, in a direction roughly

parallel to the projecting ends of the dorsal plates of the *Serolis*. A cocoon of an altogether exceptional shape is shown in Text-fig. 2.

Many of the cocoons were found to be empty, while others contained what were regarded as eggs. With the eggs there was sometimes a certain amount of amorphous material which was suspected to be the remains of the parent animal.

THE ADULT WORM.

An extensive search for the worm that makes these spiral cocoons yielded only the most meagre results. Although many cocoons taken at 12 stations, covering every month of the year except February, April, August and September, were examined, only on one fortunate occasion was a single cocoon found which was occupied by a recognizable worm-like object. This came from a haul made on 31 May, but the date probably has no significance. Cocoons containing eggs



TEXT-FIG. 3.—Anterior (A) and posterior (B) extremities of worm extracted from cocoon (from a whole preparation). *g*, genital duct; *o*, flattened ovules.

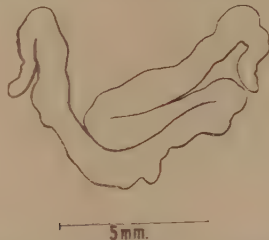
occurred in all the months for which material was available, and it appears fairly certain that the animal, like the *Serolis* which serves as its host, has no special breeding-season, and that some breeding is taking place all the year round. Although a special search was made through many samples of residue from hauls that contained the cocoons, no Turbellaria, Nemertines or other animals were ever found free in them that could be supposed to be the parent worms.

The single specimen found in a cocoon was in such a fragile condition that it was only extracted with great difficulty and in pieces. The animal measured about 12 mm. in length and 1 mm. in maximum thickness. It was cylindrical, relatively broad and blunt at what is believed to be the posterior end, which lay at the inner end of the coiled cocoon, and more tapering at the other end, which lay near the opening. This particular cocoon did not, apparently, contain any eggs. The anatomy and histology of the worm will be discussed later.

DEVELOPMENT.

The eggs contained in the cocoons were not sufficiently well preserved for detailed cytological study, and it has not been possible to follow the stages of development. One fortunate find, however, was made. One cocoon, from

a haul made on 15 July, was found to contain eggs in a much more advanced state of development than any of the others seen, with larvae apparently just hatching out from them. These larvae (Text-fig. 7) are somewhat, 'slipper-shaped' little organisms, ciliated externally, and rather closely resembling the type of larva known in the development of Nemertines as 'Desor's larva'. They measure, on an average, about 0.2 mm. in length and 0.06 mm. in width at the widest part. No eye-spots, mouth or pharynx have been seen. Little internal organization can be made out, but the wider half of the body, which is assumed to be the posterior half, contains considerable aggregations of cells. In the posterior quarter there is a mass of nuclei that stain deeply with carmine, and in front of this there appear to be irregular masses of less deeply staining cells.



TEXT-FIG. 4.—Outline of a worm as it lay in the thoracic cavity of *Serolis*, as seen from above.

These larvae develop in pairs in membranous capsules (Text-fig. 8). Even in the youngest capsules seen the contents appear to form two closely apposed but distinct masses, enveloped in a quantity of yolk-globules. The capsules measure, on an average, about 0.15 mm. in diameter, and each larva seems to be closely invested with another thin coat, which is ciliated.

THE PARASITIC PHASE.

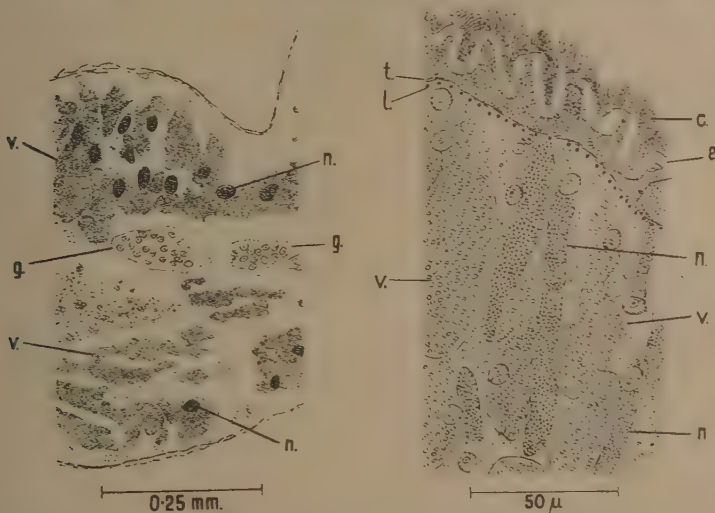
The type of development just described agrees very closely with that described by Caullery and Mesnil (1903) for *Fecampia erythrocephala* Giard and *F. xanthocephala* Caullery and Mesnil. The former species is parasitic at first in the body-cavity of crabs (*Carcinus maenas*, *Cancer pagurus*, *Eupagurus bernhardus*), the latter in the body-cavity of an Isopod (*Idotea neglecta*). Their cocoons are not attached to the hosts, but to stones and other objects. It had not previously been suspected that the present form was at any stage an internal parasite of the *Serolis*, but when the resemblance to *Fecampia* was realized, a search for the parasitic form was made. By examining a large number of *Serolis schythei* by transparency over an electric light, it was found that a very small proportion of them showed a shadow in the thoracic region which was not present in others. On dissecting these individuals a worm-like object was found lying in the thoracic cavity of each, which proved to be similar in structure to the specimen previously found in a cocoon. These parasitic forms were found in six of 500 specimens of *Serolis* from Station WS 784 (5 Dec. 1931), and in one of 25 specimens from Station WS 219 (3 June 1928). These figures, such as they are, suggest a percentage of infection of about 1.3. The worms occurred both in males and in non-ovigerous females, but were not found in ovigerous females or in specimens carrying cocoons. It seems probable that the female *Serolis* is rendered sterile by the presence of the worm.

The worms lay in a variety of irregular postures in the body-cavity of their hosts, but were usually in close contact with the ventral body-wall. They were extremely fragile (probably largely because of imperfect preservation, but partly because of their own very delicate structure), and it was found impossible

to remove them entire and undamaged. Text-fig. 4 shows in outline the position assumed by one worm in the body-cavity of the host. The worms do not retain a cylindrical shape when preserved *in situ*, but are crumpled and flattened into very irregular forms. They show no trace of pigmentation, even at the anterior extremity, such as occurs in the known species of *Fecampia*, but, as they had been kept in alcohol for a long period, any pigment that might have been present originally would probably have disappeared.

ANATOMY AND HISTOLOGY.

The anatomy of the worm is very obscure, and evidently requires living material or much better-preserved specimens for its proper elucidation. Whole preparations, stained with Mayer's paracarmine, were made of the specimen found in a cocoon and of two of those found in the body-cavity of *Serolis*, but their extremely fragile nature made the preparations almost useless. No mouth, pharynx or gut could be distinguished. In the specimen from the cocoon (Text-fig. 3, B) at what is presumed to be the posterior extremity, there is



TEXT-FIG. 5.—Portion of a longitudinal section of a worm in the parasitic phase. *g, g*, portions of genital gland; *n, n*, nidamental cells; *v, v*, lobes of vitelline cells.

TEXT-FIG. 6.—Portion of an oblique transverse section of the adult worm found in a cocoon. *c*, cilia; *e*, epithelium; *l*, longitudinal muscle-fibres; *n, n*, nidamental cells; *t*, transverse muscle-fibres; *v, v*, lobes of vitelline cells.

a suggestion of a terminal pore, which may represent the genital opening. A little in front of this two much-folded columns of crowded and deeply-staining cells (*g*) can be seen. These, in all probability, are paired genital ducts similar to those observed by Caullery and Mesnil (1903), and in the posterior part of one of them (Text-fig. 3, B, *o*) a single column of ovules, flattened into discs in the manner described, is visible.

At the other extremity of the animal a number of strands of connective tissue or muscle fibres can be seen running in different directions. Almost the whole of the body appears to be occupied by more or less spherical masses of granules or globules. In sections (Text-fig. 6) through the middle region it is found that the body is covered externally with a ciliated epithelium (*c*), below which

there are two single layers of muscle-fibres, the outer transverse and the inner longitudinal. There is no deeper musculature, and the animal's power of muscular movement must be rather feeble. There appears to be little parenchymatous or connective tissue, and most of the body is occupied by large cells of two kinds, apparently representing the nidamental cells ('cellules nidamentales') and the yolk-cells ('cellules vitellogènes') described by Caullery and Mesnil. The nidamental cells, which apparently secrete the substance of the cocoon, contain numerous granules which stain fairly deeply with paracarmine or with erythrosin, but have little affinity for haematoxylin. In the parasitic phase they appear as oval masses (Text-fig. 5, *n*), scattered irregularly about among the vitelline masses, and do not appear to have any special connection with the subepithelial layer of the body. In the worm taken from a cocoon, however (Text-fig. 6, *n*), they appear to have become elongated and to extend right up to the subepithelial muscle-layer, externally to which there seems to be a great accumulation of granules similar to those contained in the cells themselves. These granules seem to work their way through the epithelium, and many are



TEXT-FIG. 7.—Larva freed from capsule.

TEXT-FIG. 8.—Capsule containing a pair of larvae. (The wall of the capsule has been damaged).

found among the cilia on its surface. The yolk-cells form irregularly lobed masses (Text-figs. 5 and 6, *v*) extending inwards towards the axis of the worm, and are packed with relatively large globules which stain readily with erythrosin, and strongly with picric acid when sections stained with paracarmine are counterstained with picro-indigo-carmin. The nuclei of these cells appear, as stated by Caullery and Mesnil, to lie near the periphery of the animal, the more central portions being devoid of nuclei.

According to Caullery and Mesnil there is, in the parasitic phase of *Fecampia*, a definite axial cavity, bounded by an epithelium, and this cavity is gradually reduced by the development of the vitelline cells, its epithelium disappearing after the formation of the cocoon. In the present material no such definite axial cavity or epithelium has been observed. In the parasitic phase, however, there seems to be an ill-defined axial space, and in some sections portions of what may be the genital glands seem to lie in this space (Text-fig. 5, *g*). It has not been possible to trace the course of these glands or to discover how their products reach the exterior. The posterior extremity of the parasitic specimen sectioned was unfortunately lost during the process of embedding.



Group of *Serolis schythei* bearing cocoons.



A single cocoon in situ on Serolis schythei

The most notable feature of the species here described is the spiral shape of the cocoon. In *Fecampia erythrocephala* and *F. xanthocephala* the cocoons are flask-shaped. Giard (1886) described that of *F. erythrocephala* as shaped like a 'larve batavique' ('Prince Rupert's drop'). It is proposed to name the species from *Serolis* ***Fecampia spiralis***, sp. n.

The writer's thanks are due not only to those whose names have been mentioned, and especially to Dr. H. E. Bargmann for much help, readily given, and for her keen interest throughout this investigation; but also to Mr. M. G. Sawyers, Official Photographer, British Museum (Natural History), for the preparation of excellent photographs; and to Dr. T. J. Hart for very kindly lending the original drawing by Miss E. C. Humphreys from which the chart has been prepared. The positions of the stations have been inserted from the charts illustrating Dr. Hart's (1946) report on the trawling surveys of the 'Discovery' Expedition on the Patagonian continental shelf.

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 SHEPPARD, EDITH M. 1933. Isopod Crustacea, Part I.—The Family Serolidae. *Discovery Rep.*, **7**, pp. 253-362, Pl. 14.

EXPLANATION OF PLATES.

PLATE 3.

Group of *Serolis schythei* bearing cocoons. $\times$ about $1\frac{1}{2}$.

PLATE 4.

A single cocoon *in situ* on *Serolis schythei*. $\times$ about 13.

THE CHARACTER OF THE EARLY EUROPEAN POTATO

By R. N. SALAMAN and J. G. HAWKES

(Plates 5-11 and 9 text-figures.)

[Read 20 January 1949.]

Recently one of us published evidence on the origin of the European Potato* based on an analysis of the leaf characters of a large collection of cultivated potatoes collected in Bolivia, Peru, Ecuador and Colombia by Dr. J. G. Hawkes and Mr. E. K. Balls†. A study of the material proved the existence of wide variation occurring within the varietal range of what has hitherto been spoken of as the species *Solanum andigenum* which in its commonly accepted form differs in many details from our domestic potato, *Solanum tuberosum*. It was found that, as the distance from the assumed centre of distribution of the species, viz., Lake Titicaca, increased in a northerly or southerly direction, the greater was the proportion of those forms whose leaf characters approximated more closely to that of our own domestic varieties.

* Salaman, R.N. The Early European Potato: its character and place of origin. *Journ. Linn. Soc. Bot.* **53** (No. 348), pp. 1-27.

† See: Potato Collecting Expeditions in Mexico and South America: Systematic classification of the Collections. *Bull. of Imperial Bureau of Plant Breeding and Genetics*, 1944.

The material was arbitrarily divided into six groups, Nos. I-III may be described as being typical *S. andigenum* forms and accounted for 95 per cent. of the varieties collected in Southern Bolivia and Northern Argentina ; 73 per cent. of those in Central and Southern Peru ; 35 per cent. of those in Ecuador, and 30 per cent. of those in Colombia.

In all three groups the leaf itself is long and narrow ; the lateral leaflets mounted on relatively long petiolules tend to project more or less at right angles with the rachis and are themselves narrow with pointed apices.

The occurrence of folioles is variable : in the No. I group they are few and small, in No. II they may be somewhat bigger and more frequent, whilst in the No. III group they tend to be larger and are often numerous. In several examples of the *S. andigenum* Group III the folioles may be borne on the lateral petiolules as well as on the rachis, with the result that a close mat of leafage may be developed along either side of the rachis. Such a development, however, does not lead to a truly 'closed' leaf because the lateral leaflets are sufficiently widely spaced on the rachis as to preclude overlap ; indeed they rarely come into contact with one another.

Group No. IV is the largest and most widely distributed of the six groups : its members are distinguished from those in Group III by the relatively shorter length of the petiolule, the lesser relative length of the internodes on the rachis, and the greater width of the primary leaflets. There are usually four pairs of primary leaflets which are set at a sub-acute angle with the rachis, hence some slight overlapping may occur, but not enough to convert the leaf to one of the 'closed' type. The occurrence of secondary leaflets springing directly from the rachis is variable : in some varieties they are scarcely developed ; in others they may be more numerous and of medium size. The entire leaf is relatively wider and shorter than those of Groups I-III but considerably longer and narrower than those of Groups V or VI.

It was shown that the incidence of the leaf types of Groups Nos. IV-VI increases as we proceed from the Titicacan region northwards ; that of No. IV accounting for 5 per cent. of the varieties collected in Southern Bolivia and Argentina, 25, 27, 50 and 47 per cent. of those from North and Central Bolivia, Central and Southern Peru, Ecuador and Colombia respectively.

The Group IV leaf type may be regarded as an intermediate one bridging the gulf between the typical *S. andigenum* forms and those plants with larger and more fully developed leaves to which we in this country have been accustomed for a very long time.

The leaf type of Group V differs but little from our domestic varieties such as 'Great Scot' or 'Majestic', except that it is borne on more slender stems. Plants with the same or a more condensed style of leaf but mounted on thicker and more fleshy stems fall into Group VI. The members of this latter class are indistinguishable from the common run of our domestic varieties.

The change in leaf type which brings about the approximation and the ultimate identification of the *S. andigenum* and *S. tuberosum* types of potato is essentially one in which the lateral and apical leaflets increase in absolute area, whilst the length of the rachis relative to the length of the leaflets is reduced. In other words, the area of the chlorophyll bearing tissue of the leaf is increased absolutely as we pass from a lower to a higher group, whilst the leaves of the individual plants are condensed.

A simple measurement, viz., the ratio between the length of the 2nd left lateral leaflet (the first is not used because it is not infrequently partially fused with the terminal) and the distance between the points of attachment on the rachis of the first pair of leaflets and that of the 4th pair, supplies a numerical measure which is of considerable value in distinguishing leaf types and which we have ventured to call the Foliar Index.

In order to secure uniformity, the leaf chosen for measurement has been

either the third from the apex or a leaf below it ; the object is to measure an adult expanded leaf, for with such the index of any particular variety is constant within a few points.

Herbarium material and even photographs of leaves lend themselves readily to the calculation of this Foliar Index.

The values of the indices of the different classes of varieties under review are set out in Table I. The wide range of variation observed within Groups V and VI is some measure of the field in which selectionists consciously and unconsciously have striven to create varieties suitable to the growing demands of a public which, having first entertained the potato as a luxury, ended by promoting it to the position of one of the major staple articles of the people's dietary.

TABLE I.—Foliar Indices of Groups and Domestic Varieties.

Group	No. of Plants	Average	Range
III	19	61	43-70
IV	18	65	54-79
V and VI	12	90	80-110
Domestic Varieties	23	89	73-116

Speculation as to the nature and affinities of the earliest potatoes introduced into Europe has taken on a new aspect since one of us (J. G. H.) discovered in the Museum National d'Histoire Naturelle, two Herbarium specimens collected by Sébastien Vaillant (1669-1720) from the environs of Paris.

Shortly after this happy find, Dr. Hawkes departed for Colombia, and the task of searching for further evidence on this side of the Atlantic and presenting the results, was left to the senior author.

Omitting herbarium examples collected after the middle of the eighteenth century, it has been our good fortune to obtain photographs or rubbings and sometimes both, of eighteen herbarium specimens preserved during a period of some 150 years, i.e., between about 1600 and 1750. A detailed list of these is recorded in Table II.

It is common knowledge that Clusius, the first European savant to receive the potato outside Spain recorded its appearance in an aquarelle which still exists in the Plantin Museum ; it is difficult and perhaps dangerous to deduce from evidence of this kind rigid conclusions as to the character and origin of the plant. But at least it may be said that the leaf type of Clusius' aquarelle corresponds to that of Group III or IV, with a Foliar Index of 33 which although abnormally low and doubtless unreliable, is at least evidence that this potato plant was a long way removed from our present-day varieties with a minimum index of 73. In this relation, it should be pointed out that the woodcuts illustrating the potato which the great herbalists have left us are, in respect of their long drawn out leaves, the wide spacing and absence of overlap of their leaflets, all frankly *S. andigenum*-like. Such evidence, by itself, would not be of much moment, but when we find it corroborated by the dried herbarium specimens of the same period, it assumes a much increased importance.

The next to describe the potato was Caspar Bauhin, and the earliest herbarium specimen we have succeeded in tracking down is one put up by this master and labelled in his own hand, see Plate 5. The question naturally arises : does this specimen correspond with the description of 1596 in the *Phytopinax*, or to that in the *Prodromos* of 1620, or to neither ?

Before arriving at any decision it would be well to consider whether Bauhin was dealing with seedling plants of his own raising or with plants grown from tubers. Bauhin's own statement in the *Phytopinax* leaves one in little doubt. 'I received some of the seed of the plant which is called Pappas . . . Sown in our garden it grows into a sort of branching bush ; it did the same in the garden of Dr. Martin Chmielecius with whom it produced a white flower . . . the illustrious Dr. Laurent Scholtz of Breslau in whose well kept garden it was grown sent to me as a token of our friendship a coloured drawing of the plant, but this displayed neither fruit nor tubers.'

Although the word 'seed' was often used loosely in regard to the potato for true flower-seed and seed tuber alike, in this case the weight of evidence is strongly in favour of the former interpretation. In the first place Bauhin states he received seed and sowed—not planted—it. Then the plant grew into a many branching bush, which is characteristic of strong growing first season potato seedling plants ; moreover, seed, presumably from the same source, behaved similarly in the garden of his friend and, what is most significant, produced white flowers, whilst Bauhin's bore purple ones. In fact, Bauhin and his friend were working with a seedling family in which a normal segregation of characters was taking place and, as if to clinch the argument, he adds that his friend Scholtz raised a plant which developed neither flower nor tuber, a phenomenon which all potato breeders will recognize as a not uncommon experience. We may therefore conclude that Bauhin's description in the *Phytopinax* relates to a plant raised from true seed.

Whence did Bauhin and his two friends obtain this seed ? Roze * does not hesitate to claim that all three received their seed from Clusius who stated that he distributed seed amongst his friends. It is true that he mentions only Dr. John Hogeland but, as if to recompense us for not recording the others, he proceeds to tell us that Hogeland's plant yielded no tubers and bore white flowers, whereas on Clusius' potato plant they were purple, all of which lends support to Roze's view.

If, then, the potato of the *Phytopinax* was a true seedling, what was the status of that described in the *Prodromos* ? Two things may be said at once : this latter potato was quite distinct from that described in the earlier work as is shown by the fact that apart from minor differences the leaf of the latter was described as being as long as the breadth of one's hand, i.e., 4 in. whilst the length of the *Prodromos* leaf was equal to the length of a hand, viz. 8 in. It should, however, be noted that there is reason to think that the potato of the *Prodromos* may not be a single plant but consists really of two sister seedlings which shared the same bed. The mistake was not discovered but when the tops died down, red and 'black', i.e., deep purple tubers of extremely variable size and shape appeared to have been carried on one and the same root. Here, again, breeders will recall their own experiences of similar blunders.

If we agree that Bauhin's plants were all true seedlings, it follows that there is no necessity to assume that those he described in his works or preserved in his Herbarium were necessarily of one and the same clone, the probability is that they were all siblings of a single selfed parent stock.

Bauhin's herbarium specimen consists of four leaves ; three are furnished with four pairs of lateral leaflets each and one with a diminutive fifth pair. In all of the four leaves very small paired secondary leaflets, or folioles, occur between the main laterals. Mounted on a long stalk which probably overtopped the plant, is a large number of flowers and buds. The importance to us of Bauhin's specimen lies in the fact that it is a perfect example of a Group III *S. andigenum* potato and that it has a Foliar Index of 55.

* Roze, E. (1898) *Histoire de la Pomme de Terre*. Rothschild, Paris, p. 87.



Fig 1



Fig 2

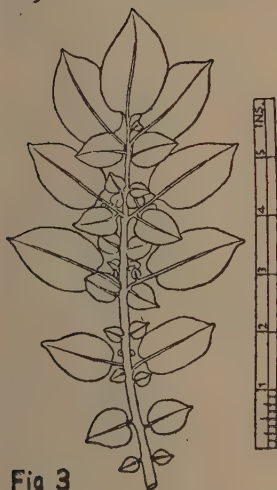


Fig 3

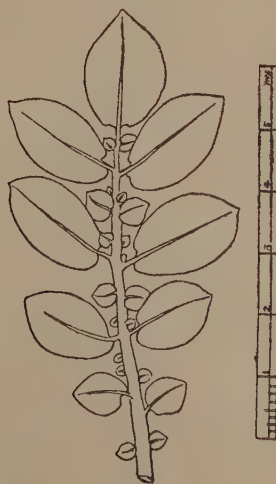


Fig 4

FIG. 1.—A variety from Pancartambo, near Cuzco, Peru. Foliar Index 65. Group I.
 FIG. 2.—Variety 'Puca Imilla' (Red girl), from Cochabamba, Bolivia. Folia Index 70. Group IV. FIG. 3.—Variety 'Sabanera,' from central Colombia. Foliar Index 43. Group III. FIG. 4.—Variety 'Arblona,' from Soto Boyacca, Colombia. Folia Index 50. Group II.

TABLE II. Showing the characters of the leaf as described in the *Phytopinax* and *Prodromos*; eighteen herbarium specimens dating between 1600 and 1750, and that of the domestic variety, 'Majestic'.

Printed Herbals	Place of Origin	Date	Length of leaf	No. of pairs of leaflets	Attachment of leaflets opp. altern.	No. of pairs of 2nd y. leaflets	Relative size of Foliolae small medium large	Length of Petiole long short	Foliar Index	Type Group	Plate No.
Caspar Bauhin 'Phytopinax'	Basle, Switzerland	1596	7-8 cm.	3-4	— +	1.	+ — —	—	—	—	—
Caspar Bauhin 'Prodromos'	Basle, Switzerland	1620	19 cm.	3-4	— —	1	— — —	—	—	—	—
Collector and Reference											
Caspar Bauhin Basle University	Basle, Switzerland	c. 1620	22 cm.	4-5	+	—	+	—	55	III	5
Joachim Burser Bot. Mus. Uppsala University	Uppsala, Sweden	c. 1620	17 cm.	3	+	1	—	—	80	V	6
Jacob Bobart senr. Bedford	Oxford, England	c. 1650	12 cm.	3	— +	1	—	—	63	IV	—
Johann Elsholz Bot. Mus. Berlin	Germany.	c. 1650	23 cm.	4	+	2	—	+	58	III	11a
Herbarium Sloane, B.M. vol. 44, p. 33	? England	a. 1660	23 cm.	4	+	1	—	+	53	III	—
Leonard Plukenet Herbarium Sloane, B.M. vol. 83, p. 63	Hertfordsh., England	c. 1670	? 18 cm.	4	—	1	—	—	72	IV	9
William Charleton Herbarium Sloane, B.M. vol. 51, p. 10	Montpellier, France	c. 1670	? 30 cm.	3	— +	2	—	+	? 50	III	—

HORTI SICCI.

Jacob Bobart senr. (?) Morrison Herbarium, Bot. School, Oxford	Oxford, England	c. 1670	?	10 cm.	4	+	—	2	+	—	—	—	—	+	85	V	—
Edward Morgan Bodley's Library, Oxford vol. iii, fol. 1510	London, England	c. 1672	?	16 cm.	4	+	—	1	+	—	—	—	—	+	66	IV	—
Jacob Bobart senr. (?) Shrewsbury School, vol. i, fol. 39	Oxford England	1676		12 cm.	4	+	—	1	+	—	—	—	—	+	60	IV	8
Sébastien Vaillant (1) Mus. Nat. hist. nat., Paris	Environ of Paris, France	c. 1700		21 cm.	4-5	+	—	2	—	—	—	—	+	—	52	III	7 ^a
Sébastien Vaillant (2) Mus. Nat. hist. nat., Paris	Environ of Paris, France	c. 1700		24 cm.	4	+	—	2	+	—	—	—	—	+	51	III	7 ^b
William Sherard Bot. School, Oxford	? Oxford, England	c. 1700	?	13 cm.	4	+	—	1	+	—	—	—	—	+	90	VI	10 ^b
Hermann Boerhaave Herbarium Sloane, B.M. vol. ii, p. 49	Leyden, Holland	c. 1720	?	18 cm.	3	—	—	1	+	—	—	—	—	+	65	III	—
Richard Rawlinson Ashmolean Museum, Oxford vol. iii, fol. 68	? Oxford, England	c. 1730	?	12 cm.	3	+	—	1	+	—	—	—	—	+	73	IV	—
Samuel Downes Shrewsbury School	? England	a. 1731		11 cm.	3	+	—	1	+	—	—	—	—	+	82	V	—
Unknown Howlett Collection, vol. iv, fol. 52 Bodley's Library, Oxford	? England	c. 1700	?	18 cm.	4	+	—	1	—	—	—	—	—	+	68	IV	10 ^a
Carl Linnaeus	Leyden, Holland	c. 1750		14 cm.	3-4	+	—	1	+	—	—	—	—	+	73	IV	11 ^b
MAJESTIC	Barley, Herts England	1948		26 cm.	5	+	—	1	+	—	—	—	—	+	87	VI	—

In Table II will be found set out in detail the leaf characters of this and 17 other herbarium specimens of the potato besides an analysis of the descriptions to be found in Bauhin's two great works. And lastly, for the purpose of comparison, there is displayed the characters of a leaf of the domestic variety, 'Majestic', so widely grown in this country. It would have been possible to substitute others with a more condensed leaf and a higher Foliar Index, but 'Majestic' has been selected because it still retains traces of its *S. andigenum* origin.

A comparison of the various features of the Bauhin's specimen and the description to be found in his two great works makes it abundantly clear that the dried specimen, Plate 5, whilst completely distinct from the plant described in the *Phytopinax* (1596), might well be the model from which the description in the *Prodromos* (1620) has been derived.

The second herbarium specimen (Plate 6) in Table II is that which was mounted by Joachim Burser, a well-known botanist who died in 1639. It is

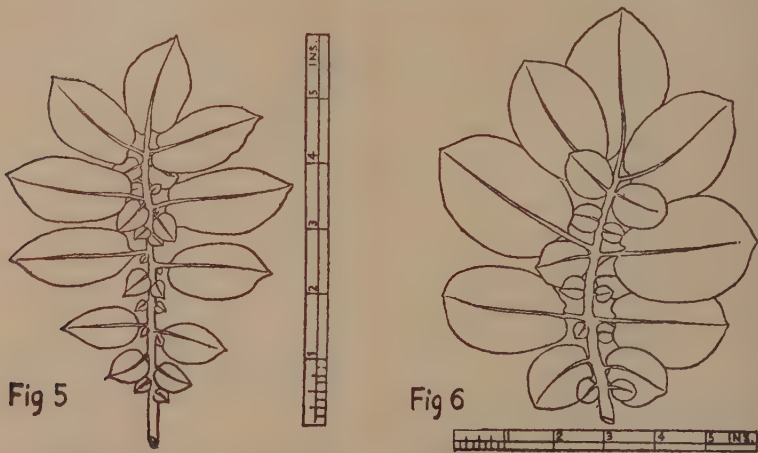


FIG. 5.—Variety 'Pali,' from Suere, Bolivia. Foliar Index 67. Group IV. FIG. 6.—A seedling of 'Argentina,' from Caldera, Cundimarca. Foliar Index 82. Group V.

probable that Burser obtained his seed—whether true flower seed or seed tuber—from Bauhin whose pupil and friend he was. If that assumption is correct, then he must have received it prior to 1629, the date of Bauhin's death.

Although the specimen is preserved to the University of Uppsala, that fact affords no evidence as to its provenance. Burser had gathered together in 25 volumes a great Herbarium; against each specimen he noted the sites where such plants were to be found; and in the case of the potato the reference is to gardens in Switzerland, Denmark, Meissen, etc. In the war between Sweden and Denmark (1658), the former seized this Herbarium as booty and removed it to Uppsala, where 23 of the volumes are still to be found; the remaining 2 were destroyed by fire.

The Burser specimen differs profoundly both from Bauhin's specimen and from the description given in the *Prodromos*. On the other hand, it can be likened to the description in the *Phytopinax* of 1596. It is true there are discrepancies between the two but such might be explained by the fact—if it is one—that Burser's potato was a sister seedling of Bauhin's. In either case a date prior to 1620 might be ascribed to it,

There is one feature about Burser's specimen which gives it a special importance in the early history of the potato in Europe. Whilst all the later continental specimens we shall consider are in varying degree closely akin to the typical *S. andigenum* stocks of South America, as evidenced by the lower grade of their leaf type and in particular by their low Foliar Index, in Burser's specimen the leaf is seen to approximate more closely to the type common to all our present-day domestic varieties, a fact which is evidenced by its Foliar Index of 80, and its inclusion in the ranks of Grade V.

The assumption that both Bauhin's and Burser's potato plants are a group of related seedlings helps us to understand the course of development which was proceeding both on the Continent and in England so far as it is recorded in our collection of herbarium material. It may be but a fleeting view, but enough to allow us to catch a glimpse of the influences bearing on the evolution of the potato as a food crop.



FIG. 7.—Outline of leaf of 'Ulster Chieftain.' Foliar Index = $\frac{A}{B} \times 100 = 88$.

The key to the problem of this evolution lies in the fact that a heavy tuber crop maturing at a considerably earlier date than the short-day '*andigenums*' do in our latitudes, requires a correspondingly larger leaf area for the manufacture of the necessary sugar and starch. This can be achieved either by a multi-branched bushy plant with small open leaves, or by a smaller plant with a few stout and more or less upright stems furnished with larger and more condensed leaves, the former will bear numerous but small, the latter few but large tubers. It is this latter type, so much more suitable for cultivation in the garden and to a still greater degree in the field, which through the skill of the plant breeder ultimately won the day.

That this procedure was not formulated till long after the arrival of the potato in Europe appears from a study of the early descriptions of the potato whether by Clusius, Gerard, the Bauhins, or Parkinson. All of them delighted in their bushy plants with long trailing stems which in Burgundy and elsewhere were layered to the ground at successive intervals to obtain more crop. Indeed

these authors boasted of the 50–100 odd tubers their plants bore. Even as late as 1710, if Salmon is to be trusted, the potato still retained its original and unreformed character.

The victory of the smaller and more concentrated type of plant was made possible by its association with a large condensed form of leaf. Hence it is that by watching the sequence of the Foliar Indices we obtain a conspectus of what was occurring throughout the formative period between the years 1600 and 1750.

Exclusive of Burser's Uppsala potato we have discovered (see Table II) six other herbarium specimens collected from the Continent. The earliest is that set up by Elsholz prior to 1653. Its provenance is Germany but exactly where, one does not know. The specimen (Plate 11 *a*.) is an unmistakeable *S. andigenum* type, displaying the long drawn out leaf with four or five pairs of lateral leaflets mounted on long petiolules commonly met with in Group III. The Foliar Index is 58.

The next in sequence of date is a specimen mounted by Charleton from a plant grown in Montpellier, France. As Charleton was working under Tournefort at the local University prior to 1673 we may provisionally date his specimen as c. 1670. The plant displays most of the characteristic features of the *S. andigenum* and falls naturally into our Group III, with a Foliar Index of 50 to which its widely separated leaflets, its long petiolules and its low Foliar Index conform. At the same time its large sized leaflets give it an affinity with types more commonly to be found in Group IV.

Vaillant's specimen No. 1 (Plate 7, fig. *a*) dating from about 1700, is identical in every feature, including the Foliar Index 52, with the specimen put up by Bauhin a hundred years earlier. It would be of great interest were we to know whether this is due to it being a direct tuber descendant of the former, or the result of a casual likeness between two seedlings widely separated as to the date of their birth. Vaillant's second specimen (Plate 7, fig. *b*) although sharing a similar Foliar Index to the former, is distinct. Like the Montpellier specimen, both those of Vaillant's are typical *S. andigenum* plants of the Group III type.

From Leyden in Holland we have a specimen collected by the botanist Hermann Boerhaave in about 1720. This specimen is distinct from any of the preceding ones but like them displays an *S. andigenum* type corresponding to Group III, with a Foliar Index of 65.

Another Leyden potato (Plate 11 *b*) has a dual interest : it served Linnaeus as the type specimen for his *Species Plantarum* 1753, and in its leaf character recalls the Burser potato (Plate 6) of more than a century earlier. Like this latter, its foliage resembles that of our modern potato much more closely than does that of any to which reference has so far been made ; indeed it would seem to bridge the gap between Groups IV and V, a position which accords well with its Foliar Index of 73.

It may be the poverty of our record rather than a true reflection of the state of potato culture in Western Europe during the eighteenth century, but we are left with the impression that up till then no real advance towards the evolution of more suitable domestic varieties had been achieved on the Continent. It is therefore of particular interest to compare this situation with that which our herbarium collections record in Great Britain.

In England potato culture began with Gerard's tubers grown in his Holborn garden, but what the character of his plant, its group, or its Foliar Index, are alike unknown. We can however be certain that it differed from Clusius' potato. It must be assumed, until we have evidence to the contrary, that all the potatoes that were grown in England, Wales and Ireland in the seventeenth century took their origin from this one plant—at least we know of no other introduction. The earliest herbarium specimen in our collection is that which was, we may suppose, put up under the authority of Jacob Bobart senior in the Bedfordshire Hortus Siccus, seeing the labels are written twice, once by Bobart

senior and again by his son. This potato was presumably grown in the Oxford Physic Garden and its date must be after 1632, the year Bobart senior took over control of the gardens, and somewhere about 1658, the year when his son began to collaborate with him on the Catalogue of the Collection. The specimen is distinct from any of the continental ones we have been discussing though it has some affinity with the Burser specimen from which however it differs widely in respect to its Foliar Index. Its type is that of Group IV and its Index 63.

The Bobarts were apparently not content to grow but one variety, though whether they themselves raised new seedlings or obtained them from others must remain an open question. We have three specimens in all, from different collections, for which the Bobarts are responsible; the one already referred to, a second to be found in the Morison Herbarium, and a third in Shrewsbury School Library.

The Shrewsbury example (Plate 8) may well have been derived from the same plant as the Bedfordshire specimen for the two coincide in all their main features as well as in the matter of their Foliar Indices and Group, but they differ in the greater number of pairs of leaflets on most of the leaves. This



FIG. 8.—Outline of leaf from the aquarelle of Clusius' potato plant in the Plantin museum.

however may be due to the fact that the Bedfordshire specimen was not skilfully handled whilst being set up.

Before passing to the last of the specimens prepared by the Bobarts, namely, that in the Morison Herbarium, two others from the same period demand attention. The first is one collected by Edward Morgan who accompanied Thomas Johnson, the editor of the 2nd edition of Gerard, on his botanical tour through Wales in 1639. Morgan's specimen belongs to Group IV and its Foliar Index is 66: it represents an advance on the early Bobart potato. Its date may be 1672 for that is the figure inscribed on the front page of the *Hortus Siccus* in which it is contained. The second specimen (Plate 9), we owe to Leonard Plukenet (1642-1706) and is probably of a like date. Its leaf is also of the Group IV type but it shows evidence of a nearer approach to the more modern varieties, a fact which its higher Foliar Index of 72 tends to confirm.

With the Morison specimen we are on quite different ground: here we have a plant whose leaf type conforms to that of our present-day varieties, and hence it belongs to Group V, with a Foliar Index of 85.

The specimen was mounted presumably by the Bobarts about 1680. Another specimen (Plate 10, fig. *b*) preserved in the Sherard Herbarium was very likely grown in Oxford and dates from about 1700. It was derived from a similar but

probably distinct variety to the last. The leaf type is completely modern, its Foliar Index is 90, and because of its thickened stem the plant may be classed as an example of Group VI.

A similar but not identical variety is represented by a specimen put up by Samuel Downes and given to Shrewsbury School in 1731. Its Foliar Index is 82 and its leaf type that of Group V.



BARLEY, 13.9.26
F.I. 73.

Paterson's Seedling
Pepo^x 408c.17

FIG. 9.—Outline of leaf of a seedling derived from 'Paterson's Seedling' x 'Pepo,' grown at Barley, Herts. The characters have reverted to an *S. andigenum* of Group III pattern. Foliar Index 73, date 1926.

The evidence which these last three specimens afford makes it obvious that in the early decades of the eighteenth century the modern type of potato plant had already been evolved, at least in Oxford. That it was not confined to Oxford, however, may be gathered from two further specimens in the collection : one was found in the Rawlinson Collection in the Bodleian, dating from about

1730, in which we have a plant of a Group IV type with the relatively high Index of 73, and another in the Howlett Collection in Bodley's Library, of which we can only hazard the guess that it dates from the first half of the eighteenth century. This last specimen (Plate 10) is particularly interesting, for although it, too, belongs to Group IV, with an Index of 68, the large size of its leaflets and their tendency to overlap, suggest that it, too, represents a definite step forward in the development of the modern potato variety.

It should not be assumed that *S. andigenum* traits have been completely exorcised from our domestic stocks; they are occasionally revived if selection is exercised in the reverse direction. For example, in a cross between 'Pater-son's seedling' and 'Pepo', a much used paternal stock, one of us (R.N.S.) selected a seedling whose leaf is shown in text-fig. 9. The type of leaf appears to be a throwback to a Group III *S. andigenum*, from which it only differs by its higher Foliar Index of 73. An almost identical leaf type with a similar Index has been found amongst the progeny of the variety 'President' when selfed, notwithstanding that the parent plant has a Foliar Index of 100.

To sum up, we may say that evidence derived from herbarium specimens proves beyond a doubt that the earliest types of potato grown in Western Europe and England were typical of *S. andigenum*; that new varieties were continually being raised from true seed, and that by selection forms were cultivated in which a larger and more condensed type of leaf mounted on a stouter stem, was evolved. In other words, *S. andigenum* has, by selection, been converted into *S. tuberosum*. This process seems to have proceeded rather more rapidly and at an earlier date in England than in Western Europe.

EXPLANATION OF THE PLATES.

PLATE 5.

Specimen of Potato plant preserved by Caspar Bauhin. The label on left, written in his own hand: '*Solanum tuberosum* esculentum C.B.' That on the right is by Candolle, and reads: '*Solanum tuberosum*.' Foliar Index 55. Group III. Reproduced by permission of The Curator of the Herbarium, University of Basle.

PLATE 6.

Specimen of Potato plant preserved by Joachim Burser. In Burser's own hand: '*Solanum tuberosum* esculentum Bauh.' The letter 'V' is written by Olaf Rudbeck and is the species number of Bauhin's *Pinax*. Foliar Index 80. Group V. Date c. 1620. Reproduced by permission of The Curator of the Botanical Museum, Uppsala University.

PLATE 7.

- (a) Specimen of Potato plant preserved by Sébastien Vaillant. Foliar Index 52. Group III. Reproduced by permission of The Curator of the Musée National d'Histoire Naturelle.
- (b) Specimen of Potato plant preserved by Sébastien Vaillant. Foliar Index 51. Group III. Reproduced by permission of The Curator of the Musée National d'Histoire Naturelle.

PLATE 8.

Specimen of Potato plant probably set up by Jacob Bobart, senior, inscribed: '*Battatas Virginiana*; *Virginian Potatoes*.' The Hortus Siccus is prefaced on its Frontispiece as under: 'An Universal Theater of Trees, Shrubs, Plants and Flowers as well as those that are cultivated as those that grow wild.'

Collected chiefly out of the Physick Garden in Oxford and digested into an alphabetical order. Anno Domini 1676.' Foliar Index 60. Group IV. Reproduced by permission of The Librarian, Shrewsbury School.

PLATE 9.

Specimen of Potato plant collected by Leonard Plukenet and grown in a garden in Westminster or at Horn Hill, Herts. Herbarium Sloane, V. 83, p. 63. Foliar Index 73. Group IV. Reproduced by permission of the British Museum.

PLATE 10.

- (a) Specimen of Potato plant contained in the Howlett Collection of the Bodleian Library, Oxford; provenance unknown. Foliar Index 68. Group IV. Date c. 1700. Reproduced by permission of the Bodleian Library.
- (b) Specimen of Potato plant contained in the Sherard Herbarium. Foliar Index 90. Group VI. Date c. 1700. Reproduced by permission of the Regius Professor of Botany, Oxford.

PLATE 11.

- (a) Specimens of Potato plant from the Elsholz Herbarium, collected prior to 1653. By permission of Prof. Dr. Carl Snell of the Botanical Museum, Berlin.
- (b) Specimen of Potato plant from Linnaeus's Herbarium, collected about 1750. By permission of the President and Council of the Linnean Society.

Postscript

Since going to Press, we have to thank Prof. Francesco Zorzi for the photograph of a specimen from the Herbarium of Pier Fortunato of Rovigo (1639–1701), now in the possession of the Museo Civico di Storia Naturale in Verona. The specimen, which is much damaged, would seem to belong to Group IV and has a Foliar Index of 60. It differs from all those already described, by the relatively greater breadth of its leaflets.

OBITUARIES

William Borlase was born at Liskeard in Cornwall on 23 March 1860. His family soon moved to Perranporth on the North coast of the county, and William was sent to the Church Day School, the headmaster of which was Mr. William Tresidder, a good botanist. Mr. Tresidder later moved to a larger school at Goonhavern a few miles away, and William Borlase at the age of 15 became his first pupil-teacher. After some years of teaching in and out of the county, Borlase was appointed Head of the Mawnan Smith Church School not far from Falmouth, where he continued for 16 years. It was here that he began evening classes in agriculture at Falmouth. He proved himself to be a clear and interesting teacher, and in 1901 he was attached to the Truro Technical School as Agricultural Lecturer for Cornwall. In this kind of lecturing Borlase was a pioneer, and his methods were adopted by the Ministry of Agriculture on a country-wide basis. His success in stimulating young farmers to acquire a more scientific knowledge of the technical side of their business was widely recognized, and the late Sir Daniel Hall paid a striking tribute to the value of his work.

During the 1914–1918 war, Borlase was largely concerned with the setting up of parish and district agricultural committees which the Government adopted as the basis of agricultural organization throughout the country in the later war of 1939–1945.

After his retirement from the public service Borlase joined the advisory staff of Farm Industries Ltd. and continued with that firm until a few months before his death at Truro at the age of 88 on 14 December 1948.

Borlase was an active member of the Council of the Royal Institution of Cornwall and took a great interest in the history and antiquities of the county as well as in his own special botanical studies.

He was elected a Fellow of the Linnean Society in 1932 and among his best known papers were the following—contributed to the Royal Institution of Cornwall: 'The use of Shell-sand in Cornish Agriculture', 1932; 'The Flora of the Cornish Sand-dunes (towans)', 1933, accompanied by a collection of 100 species of plants from the dunes; two papers on Cornish Grasses, 1938 and 1939. A collection of about 150 species, nearly all Cornish, accompanied these papers.



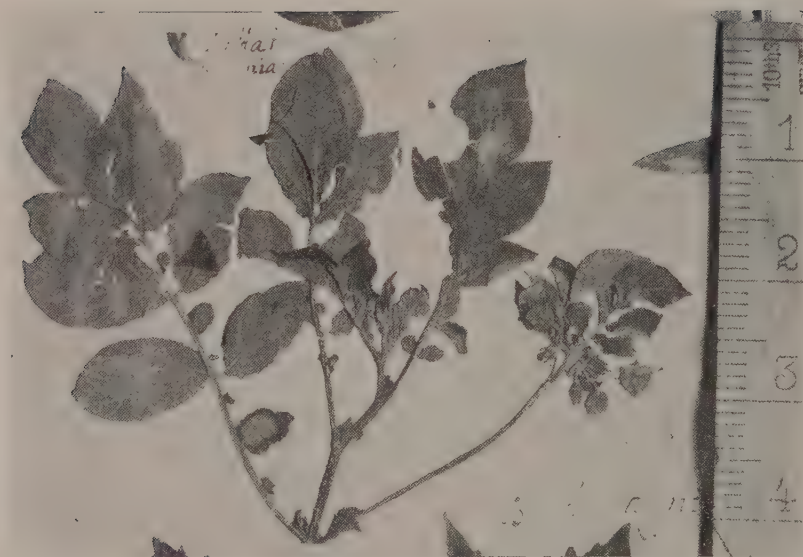
Specimen of Potato plant in Herb. Caspar Bauhin.



Specimen of Potato plant in Herb. Burser,



Specimens of Potato plants preserved by Sébastien Vaillant.



Specimen of Potato plant probably set up by Jacob Bobart senior.



Solanum tuberosum L.
Convolvulus virginianus
Yellowish. Batatas (Amur)
Hispanicum - Clus.

R. H. 675.

Specimen of Potato plant collected by Leonard Plukenet.



a. Specimen of Potato plant in the Howlett collection.



b. Specimen of Potato plant in Herb. Sherard.



a. Specimen of Potato plant preserved by Johann Elsholz.

b. Specimen of Potato plant preserved in the Linnaean Herbarium.

In 1938, Borlase was presented with the Mary Trefusis Silver Medal of the Royal Institution of Cornwall for his work in connexion with the Botany of Cornwall.

Borlase was twice married but has left no children. He was a gentle kindly man, a devout Methodist, a man who made many friends and no enemies.

J. W. HUNKIN, Bishop of Truro.

William Bathgate Cranfield was born on 1 March 1859, in London; his family moved to Enfield when he was a small boy and the rest of his long life was spent there. For the last 40 years he lived at East Lodge where he created a garden that was always a source of interest and delight to the many visitors he welcomed there. He died on 29 May 1948 in his ninetieth year, suddenly, for he had attended Committee Meetings at Chelsea Flower Show during the previous week. By profession he was an auctioneer, being senior partner in the firm of Messrs. H. E. Foster and Cranfield, but his leisure time was devoted to horticulture, in particular Daffodils, Paeonies and Irises, of which he raised a number of good varieties. He also specialized in hardy Ferns and had a unique collection of unusual forms. He was elected a Fellow of the Linnean Society in 1927, and in 1936 was awarded the Victoria Medal of Honour by the Royal Horticultural Society in recognition of his great services both as a Committee member for many years and as a very able plantsman.

VERA HIGGINS.

Miss Florence Hannah Bacon Marsh (1881–1948), born in Warwickshire, was educated privately and at one of the first co-education schools, at Hindhead. She then studied botany under Professor J. W. Carr of Nottingham University, specializing in the then rather new science of Ecology and doing research on pollen grains. Ill-health, her own and that of her family, together with the loss of the sight of one eye, obliged her to abandon what seemed certain to be a brilliant career in science. But she remained an enthusiastic field botanist and gardener all her life: became a Referee for the Wild Flower Society and a member of the Botanical Society and Exchange Club, and undertook coaching in horticulture for the examinations of the R.H.S. At the time of her death, she was engaged upon a revision of the Flora of Herefordshire. Miss Marsh was elected a Fellow of the Linnean Society on 9 May 1935. M. WIGHT.

Johan Hjort was the son of Johán Storm Aubert Hjort, Professor of Ophthalmology, and was born in Christiania. In 1887 he passed his Matriculation examination and began to study for the Medical profession, taking the first part of the Medical Examination: but he always wanted to be a biologist and he then went to Munich and studied under Richard Hertwig. He spent a short time at the Marine Biological Laboratory, Naples, studying the development of an Ascidian, *Botryllus*, and then took his doctorate degree at Munich in 1892. He returned to Norway in 1893 and was appointed Lecturer in Zoology and Curator of the Zootomical Museum in Oslo University, and in the following year succeeded G. O. Sars as Research Fellow in Fisheries. From now on his main interest was focused on the Marine Fauna and Flora, though, as he himself recorded, his work 'had two separate aims, the study of the animal life of the ocean and the discovery and development of new and better ways of carrying on the Norwegian Fishing Industries'.

In 1895–96 he studied physiological chemistry at Jena and on his return to Norway was appointed Director of the University Biological Station at Drobak.

During 1895–97 he collaborated with F. Dahl in investigating the conditions that were present off the west coast of Norway between Stavanger and Lofoten in order to discover whether seasonal changes in the hydrological conditions and the fauna of the Norwegian coast were due to incursions of water from the Polar area across the North Atlantic Drift: one result of this work was to indicate

that the changes observed in this region were dependent in the main on the Gulf Stream and the North Atlantic Drift and were not due to variations in the Polar Current.

In 1897 he investigated the Norwegian Prawn, *Pandalus borealis*, and in 1899, again in collaboration with Dahl, he investigated the animal life that is to be found in that region of the sea bottom known as Murray's 'Mud-Line'. During this work he discovered that the soft mud at the bottom of the fjords on the south-east coast of Norway was inhabited by large numbers of this Prawn and he designed a new type of net adapted for catching these Crustacea. The immediate result of this work was the establishment of a new fishery that soon grew in importance, for the annual catch in 1930 was some 2000 tons and a few years later had reached to over 4000 tons.

In 1899 Hjort persuaded the Norwegian Government to build the 'Micheal Sars' and between 1903-1905, in collaboration with the Danish Scientist, C. G. Joh. Petersen, Hjort carried out systematic investigations regarding the North Sea Fisheries; they pointed out that 'experience has shown above all that depth, temperature and salinity have the greatest influence on the occurrence of the various species of fish and on the richness of animal life', and they emphasize that the first preliminary condition of all fishery investigations must be an exact and purely geographical knowledge of the various parts of the ocean, while hydrographical investigations must also be made to provide information concerning the general distribution of the fishes. The essential necessity of this knowledge cannot be too strongly emphasized for it seems in these days to be under-rated and even overlooked in various parts of the world, in which the Fisheries have hitherto been carried out in a primitive and haphazard manner, but where economic necessity has now compelled a change to more modern and intense exploitation. In the North Sea and the North Atlantic they obtained evidence of the limits between the true Arctic fauna and the coastal bank fauna in the Norwegian Sea, limits that varied, however, in different parts of the area in accordance with differences in the strength of the oceanic currents, while the character of the sea-bottom also showed a great influence on the quantitative distribution of the fish, depressions with a muddy bottom possessing only a poor fish fauna, whereas elevations with a sand or gravel or stony bottom gave good catches. It was shown that the pelagic fishes distributed themselves in various bio-geographical regions, which are limited by the currents of water both vertically and horizontally.

The invention by Petersen of his 'Young Fish Trawl' enabled good collections to be made, at all depths, of the larval and young stages of both shallow-water and deep-sea species, and from a quantitative estimation of the number of Cod-fish ova in the surface-water Hjort was able to determine the breeding grounds of various species. He was largely responsible for inducing the International Council for the Exploration of the Sea to organize extensive investigations, extending from the Barents Sea to the Bay of Biscay: the results of these showed that each species of the family Gadidae has a characteristic spawning ground that differs from that of all the others. In the genus *Molva* even the most closely related species have their own 'territory' and it was shown that these bio-geographical regions coincide with the limits of certain definite physical conditions. The distribution of the young stages was found to be different from that of the adult but still showed similar specific differences of distribution, owing to the different requirements of each stage of development in the various species as regards the organisms on which it feeds and other data.

From a study of Norwegian Fishery Statistics Hjort concluded that the stock of fish in the ocean must fluctuate from year to year, and the development of the technique by which the age of individual fish can be determined by examination of their scales and otoliths, enabled Hjort to demonstrate that in the North Sea the Herring captured in a series of years all belonged to the same batch that

had been spawned in 1904. Similar results were obtained from a study of the Norwegian Cod. In 1914 at the invitation of the Canadian Government Hjort visited Canada and he found that conditions of life in those waters and many of the problems involved were similar to those that he had investigated in Norway, and he was able to show that the same year-class also dominated the Herring Fishery in the Gulf of St. Lawrence.

During the period in which he was attached to the Norwegian Fisheries Hjort carried out at different seasons of the year numerous cruises in the Norwegian Sea and the North Atlantic from the coasts of Norway to Iceland, Jan Mayen and Spitzbergen Islands, investigating both the hydrographic and biological conditions in this area. One of the most important of such cruises was the one undertaken in conjunction with Sir John Murray in 1910, the results of which have been given in *The Depths of the Ocean*, which has been described as the Oceanographers' Bible and most of which was written by himself. In this work he has called attention to the fact that along the continental slopes one can easily recognize different biological strata at different depths, each stratum characterized by its peculiar fish fauna, though there is a certain degree of admixture at the boundaries. In the open ocean the greatest concentration of the fish-fauna is to be found at a depth of about 200–500 m., while of northern species the maximum frequency occurs between the isotherms of 6°–8° C., at a depth of about 100 m. The most profound depths are far more thinly populated, though the deepest dwelling species appear to have the widest distribution; but the paucity of the catches, frequently consisting of single examples, renders it very difficult to decide whether individuals, taken in widely separated localities and which may present slight differences, should be referred to the same species. He makes the very significant remark, 'As to the origin of variation it is now more and more recognised, that a comprehension is only to be gained by studying the reaction of organisms *against* the influence of surroundings'. (The italics are mine, R.B.S.S.)

Hjort was one of the scientists by whose action the International Council for the Exploration of the Sea was founded in 1902, and he was appointed by the Norwegian Government to be their representative. Throughout the rest of his life he continued to be a Member of the International Council and was a dominant figure at its meetings. In 1920 he was appointed one of the Vice-Presidents and a Member of the Bureau, and in 1939 was elected President and continued to hold this post till his death. In 1916 Hjort was elected a Foreign Member of the Royal Society of London and in the same year was made an Hon. Member of the Challenger Society.

In 1919 Hjort resigned from his post of Director of Fisheries as a result of disagreement with the Norwegian Government on their policy of maintaining secrecy regarding certain negotiations between them and the British Government, in which Hjort had taken part. He then left Norway and for the next four years carried out studies in Copenhagen and Cambridge, where he became a member of Gonville and Caius College, and in 1921 he was awarded the degree of Sc.D.(Honoris Causa) of Cambridge University. In 1921 Hjort was recalled to Norway and was appointed Professor of Marine Biology at Oslo University—a post that was specially created for him.

As early as 1902 Hjort had begun to take an interest in the Whaling Industry and soon after his return to Norway in 1921 he began an intimate co-operation with the Association of Whaling Companies and played an important part in their subsequent administration and organization, that resulted in an expansion of this industry, and in 1929 he was appointed Chairman of the first Norwegian Whaling Committee and in 1926 Chairman of the International Whaling Committee set up by the International Council for the Exploration of the Sea, retaining this appointment till 1939, when he was elected President of the Council.

In 1929 he paid a visit to the Antarctic Ocean in the new factory-ship 'Vikingen' in order to study the whale-fishery and it was during the long voyages to and from this southern region that he wrote his book *The Emperor's New Clothes*, in which he has given us his views on recent developments in our knowledge of both Biology and Physics. His attitude towards many of the modern theories is sufficiently indicated by the title of this book, he himself being cast as the small boy, who exclaimed, 'Why he hasn't got any clothes on at all'! He was particularly scornful of the attitude adopted by Mendelists towards the problems of evolution and their claim that 'the facts of genetics prove that mutation is the only means by which differences originate in genes that follow Mendel's law', and he maintains that 'Mendelists study not the *origin* of species (since variations and species originate in Nature by chance) but the constancy of the genes'. He remarks 'My own view of Nature makes it difficult for me to imagine any biological solution (of the problem of evolution) which is not based upon a connection between structure and function'; and he seems to envisage the possibility that the structure of an animal may be the result of its chemical composition, for he puts forward the view that 'we must postulate a relation, strictly determined by law, between the chemical and physical structure and the structure visible to the eye. In the same way the changes that take place in an organism must go hand in hand with the formation of the new structural compounds that become incorporated in the old organisation'.

In 1936 Hjort attended the 300th Anniversary of the founding of Harvard University, and during this visit to America, by arrangement with Prof. Henry Bigelow, he was able to make a cruise in the 'Atlantis'. He had taken with him the Prawn-trawling equipment that was in use in Norway and an experienced Prawn Trawlerman. The area investigated lay to the north of Cape Cod between the coast and Jeffrey's Ledge. It was known that along this section of the American coast, that is washed by the Labrador Current, a fauna is to be found very similar to that on the coast of Norway and Spitzbergen, and the cruise was undertaken in order to investigate the possibility of establishing a new fishing industry. Hjort was able to demonstrate that here too, exactly as in the Norwegian fjords, there is a marked correlation between the percentage of organic matter in the mud and the prawn population: his Norwegian investigations had demonstrated that on these prawn grounds there is also a plentiful fish fauna, and similar results were obtained in these American waters.

I unfortunately never had the pleasure of knowing Hjort personally, but several of those who knew him well describe him as being 'a typical Viking': he was physically a big man and was a powerful and complex personality, instinctive rather than intellectual, holding his own views very strongly and almost impervious to other opinions. Withal he was very human and likeable and got on well with everyone. He was a profound believer in the importance of the individual for the advancement of Society and he published many articles in the daily press and in various journals, as well as a book 'The Unity of Science', in which he gave expression to his views.

He was elected a Foreign Member of the Linnean Society of London in 1946.

I have to thank Professor Johan T. Ruud, of the Biological Institute, Oslo, for many of the details of Hjort's life.

R. B. SEYMOUR SEWELL.

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SOME SPECIAL PUBLICATIONS.

A Catalogue of the Linnaean Herbarium, compiled and annotated by Spencer Savage, F.L.S. London, 1945. (Pp. xvi+226, frontisp., 8 plates and pull-out leaf). £3 net.

Synopses of the British Fauna :—

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General Index to the first Twenty Volumes of the Journal (Zoology) ... London, 1896. (Pp. 437.) 6s. 8d. net.

General Index to the first Twenty Volumes of the Journal (Botany) ... London, 1888. (Pp. 428.) 6s. 8d. net.

The Darwin-Wallace Celebration held on Thursday, 1st July, 1908, by The Linnean Society of London. London, 1908. (Pp. 118.) 3s. 4d. net.

[Continued overleaf.]

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Catalogue of the Manuscripts in the Library of The Linnean Society of London.—Part 1. *The Smith Papers.* (*The Correspondence and Miscellaneous Papers of Sir James Edward Smith, M.D., F.R.S., first President of the Society.*) By Warren R. Dawson, F.R.S.E. London, 1934. (Pp. 114.) 13s. 4d. net.

Catalogue of the Manuscripts in the Library of The Linnean Society of London.—Part 2. *Caroli Linnaei Determinationes in hortum siccum Joachimi Burseri.* *The text of the manuscript in the Linnaean Collections*, edited by Spencer Savage, F.L.S. London, 1937. (Pp. 78.) 13s. 4d. net.

— Part 3. *Synopsis of the Annotations by Linnaeus and contemporaries in his Library of Printed Books.* By Spencer Savage, F.L.S. London, 1940. (Pp. 20.) 6s. 8d. net.

— Part 4. *Calendar of the Ellis Manuscripts.* (*The Correspondence and Miscellaneous Papers of John Ellis, F.R.S.*) By Spencer Savage, F.L.S., Hon. Memb. Sv. Linné-sällsk. (Pp. vi, 104.) London, 1948. 25s. net.

‘A Prodrromus of the British *Hieracia*.’ By the late H. W. Pugsley, B.A., F.L.S., has been published as Vol. 54 (No. 351) of the Society’s Journal, Botany, comprising pp. iv, 356, and 17 plates. Copies are available for purchase by non-members, £3.